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THE POSTCRANIAL SKELETON OF *STYRACOSAURUS ALBERTENSIS*

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ABSTRACT

Recently discovered material of *Styracosaurus albertensis* (Dinosauria, Ceratopsidae) in combination with the partial holotype skeleton from Dinosaur Provincial Park, Alberta, permits a comprehensive description of the postcranial skeleton of this taxon for the first time. Although this study generally supports the commonly held view that the postcranial skeleton of ceratopsids is structurally conservative, a survey of what is known about the structural diversity in the ceratopsid postcranial skeleton suggests that morphological variation of potential phylogenetic significance exists. This variation includes presacral vertebral counts (both total numbers and distribution amongst the cervical, dorsal, and sacral components of the column), patterns of intervertebral fusion, as well as morphology of the cervical ribs sacrum, pelvis, scapula, and humerus.

Introduction

The holotype skull of the centrosaurine ceratopsid *Styracosaurus albertensis* (CMN 344) was collected in 1913 by C.H. Sternberg and described later the same year (Lambe, 1913), but for reasons explained elsewhere (Holmes et al., 2005), the postcranial skeleton was not collected until 1935. The postcranial skeleton was eventually reunited with the skull as a display mount in the fossil gallery of the National Museum of Natural Sciences (now the Canadian Museum of Nature) in Ottawa, but in the intervening years, it was never described. Contemporary mounting techniques that used a heavy welded supporting steel armature rendered much of the skeleton inaccessible and made a detailed description impractical. However, in 2003, the skeletal mount was disassembled and conserved, providing for the first time unfettered access to its anatomy.

Although the postcranial skeleton of CMN 344 is reasonably well preserved, it is incomplete. The tail is represented by only seven proximal vertebrae. Most of the elements of the epipodials, mani, and pedes were not recovered, and the sacrum, left ilium, and both pubes are missing (Holmes et al., 2005). This is unfortunate, as *Styracosaurus* is relatively rare compared with most other ceratopsids from the Dinosaur Park Formation of southern Alberta. The only other described postcranial skeleton attributed to this genus (*Styracosaurus* "*parksi*," Brown and Schlaikjer, 1937) is associated with a very incomplete skull, and its identity is in question (Ryan et al., 2007). In 1989, a second articulated *Styracosaurus* skeleton (TMP 1989.097.001) was collected from Dinosaur Provincial Park (DPP). Although this individual is slightly smaller than the type and apparently not fully mature, its parietal bears the parietal spikes diagnostic of *Styracosaurus* (Ryan et al., 2007). Many of the preserved elements of the postcranial skeleton, including several presacral vertebrae, ribs, right pectoral girdle and humerus, and right pubis, right ilium, and rear propodials and epipodials overlap with those of the type, thus providing useful corroboration of its identification. It also includes complete ilia, right hind foot, and tail, thus providing much new anatomical information not preserved in the holotype. Between the two specimens, virtually every part of the skeleton except the manus is preserved.

More recently, another partial skeleton (TMP 2009.080.001), that includes most of the skull and a limited number of disarticulated postcranial elements has been collected. This specimen provides anatomical corroboration and a few features not preserved or exposed in the other *Styracosaurus* skeletons.

Institutional Abbreviations

AMNH, American Museum of Natural History; CMN, Canadian Museum of Nature (formerly the National Museum

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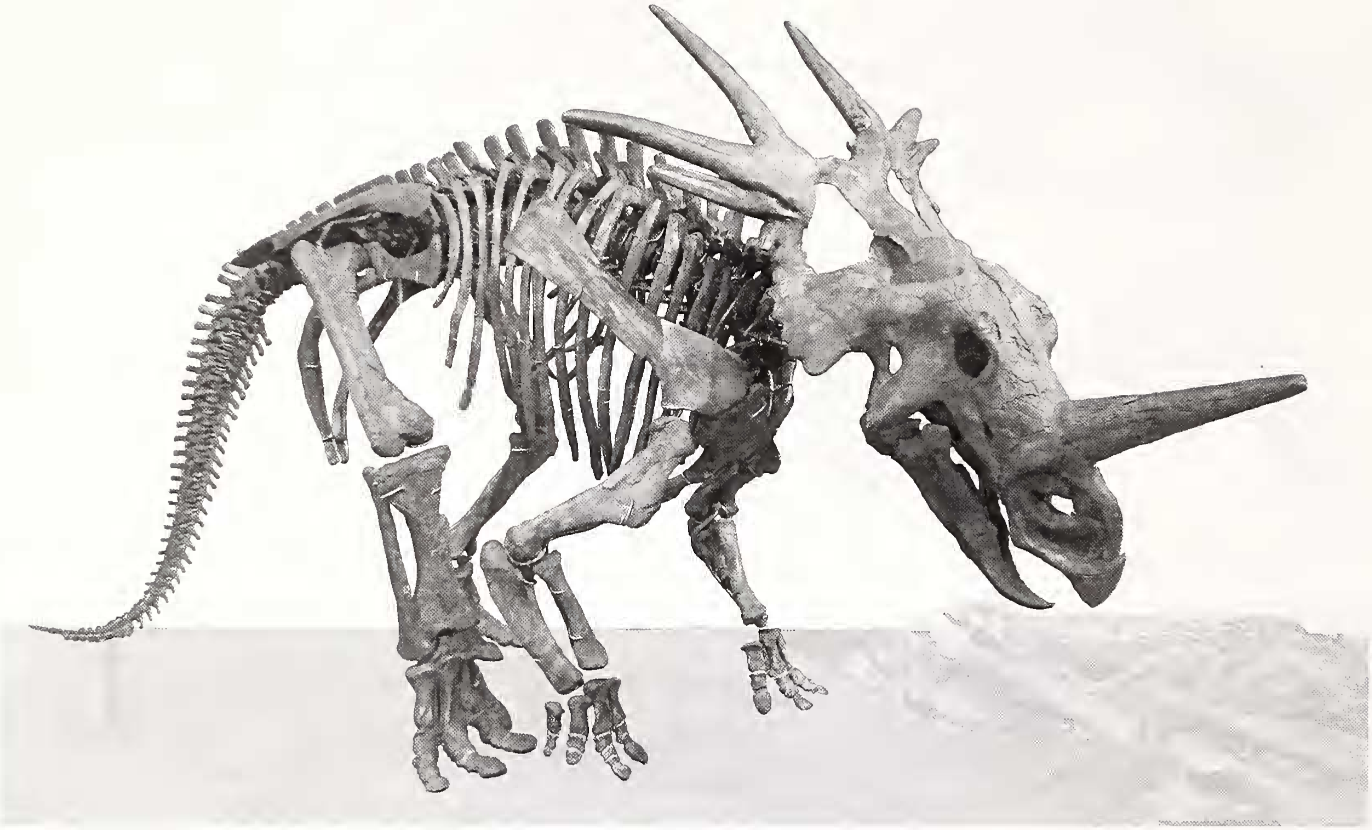

Figure 1. *Styracosaurus albertensis*, CMN 344. Mount of skeleton on exhibit at the Canadian Museum of Nature (Ottawa). Photograph taken February, 2012.

of Canada), Ottawa; **NHMUK**, Natural History Museum, London; **NSM**, National Museum of Nature and Science (formerly National Science Museum), Tokyo; **ROM**, Royal Ontario Museum, Toronto; **TMP**, Tyrrell Museum of Paleontology; **USNM**, United States National Museum, Washington.

Geology

CMN 344 was collected from the southeast quarter of section 1, TP21, R11 (Sternberg, 1950) at the extreme eastern end of what is now DPP. It occurs in the upper Dinosaur Park Formation close to prairie level in this part of the Park (708.9 masl; Currie and

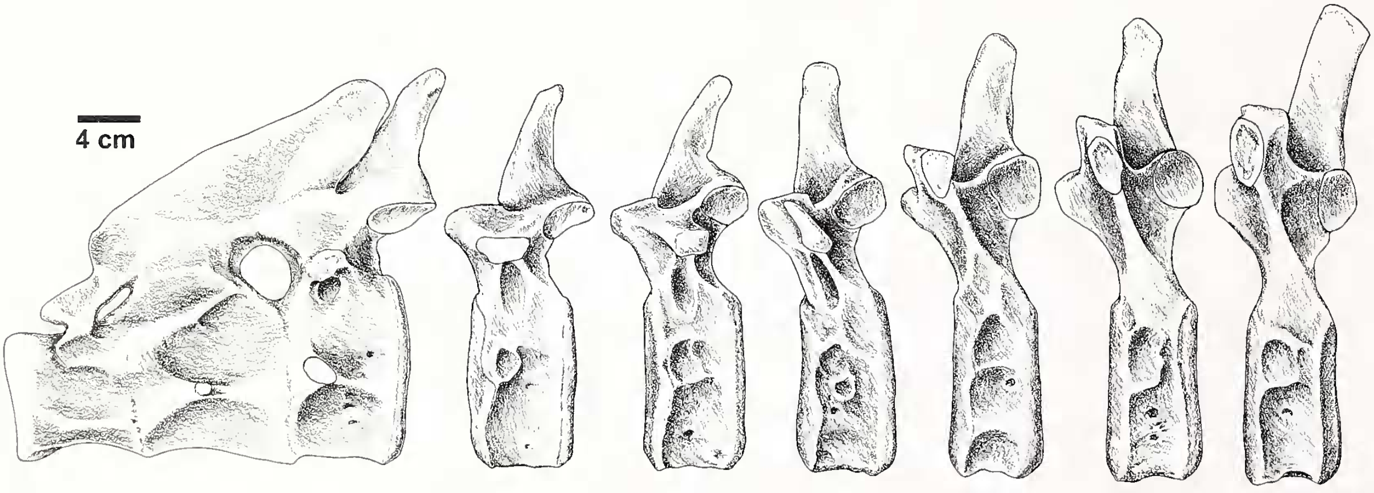

Figure 2. *Styracosaurus albertensis*, CMN 344. Cervical vertebrae (C1–C9) in left lateral view. Scale bar equals 4 cm.

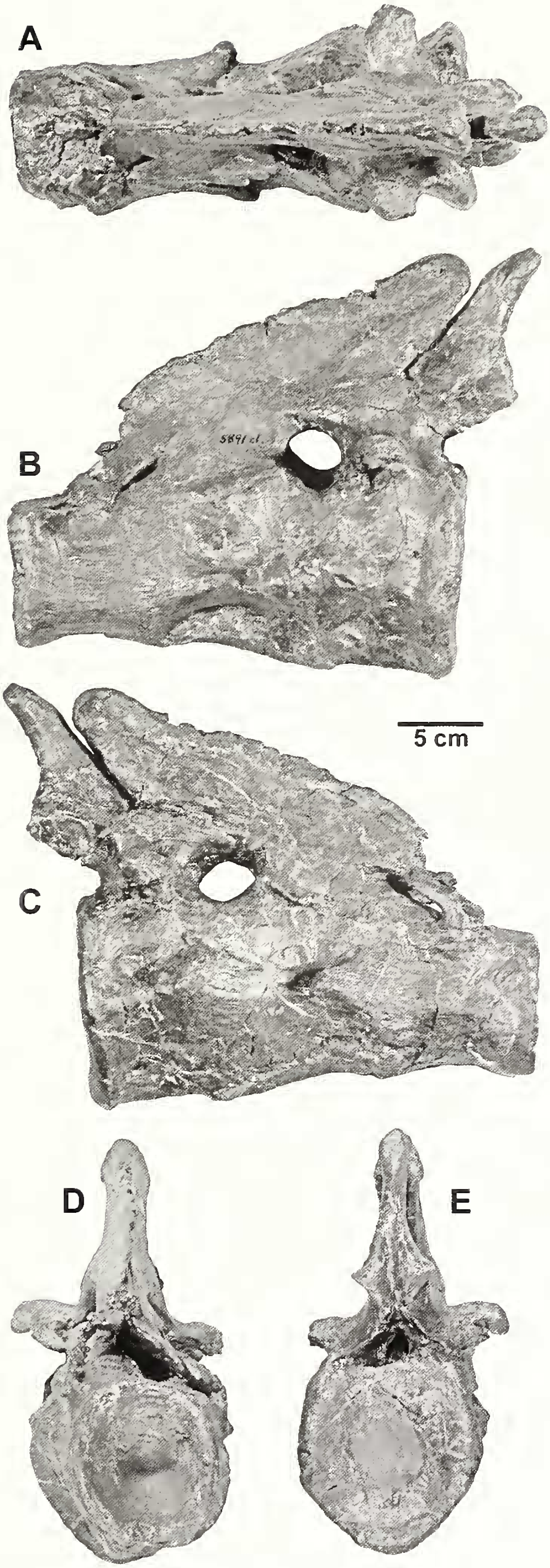

Figure 3. *Styracosaurus albertensis*, CMN 344, syncervical. A, dorsal, B, left lateral, C, right lateral, D, anterior, and E, posterior views. Scale bar equals 5 cm.

Russell, 2005), 43 m above the contact with the Oldman Formation. This places it in Dinosaur Park faunal zone 2, which is characterized by the presence of the centrosaurine ceratopsid *Styracosaurus* and the lambeosaurine *Lambeosaurus* (Ryan and Evans, 2005; Ryan, et al., 2012).

TMP 1989.097.001 was discovered at Sage Creek, near Onefour, southeastern Alberta (12, 545,414 E; 451,340 N [WGS 84]) in sediments of the Dinosaur Park Formation, less than 10 m below the Lethbridge Coal Zone (Ryan et al., 2007).

TMP 2009.080.001 was collected from Dinosaur Provincial Park, UTM 12; 461,295; 5,617,724—NAD83. The elevation was not recorded, but the field notes indicate that it occurred high in section.

Materials and Methods

Specimens examined

CMN 344—Comprises a largely complete skull with partial frill (Ryan et al, 2007), complete presacral vertebral column and partial caudal series, a set of ribs missing only the pair associated with the axis of the syncervical, right scapulocoracoid, left scapula, right sternal plate, both humeri, ulnae, and radii, right metacarpus I, left metacarpus IV, left terminal manual phalanges I and II, right ilium, both ischia, femora, tibiae, left fibula, and left metacarpus II (Figures 1–23; Table 1).

TMP 1989.097.001—Comprises a partial skull (Ryan et al., 2007) and a mostly articulated postcranial skeleton including a partial presacral vertebral column scattered ribs, a complete tail, right scapulocoracoid, a partly exposed left scapulocoracoid, both humeri, a complete pelvis (although the sacrum is not exposed), both femora, right tibia and fibula, and the compete right metatarsus and pes (Figures 24–35; Table 1).

TMP 2009.080.001—Comprises a large, virtually complete skull and associated cervical vertebrae, sacrum, and scapula.

Methods

Although the type postcranial skeleton was collected in 1935, a comprehensive description has been hampered by its use as a display mount at the Victoria Memorial Museum Building in Ottawa. When the old Earth Sciences gallery was dismantled in the early 2000's, this material was rendered accessible to study for the first time. Following disassembly of the display mount, the elements were conserved and made available for study for several months before a new mount was constructed (Figure 1). This made it possible to determine the extent of reconstruction, and eliminated the risk that plaster elements, fabricated to replace missing bones, might be included in the description. Individual elements were photographed from as many perspectives as practical. Many of these images were published in Holmes et al. (2005). As the vertebrae and ribs were particularly prone to distortion, an attempt was made to reconstruct their original shapes. These reconstructions are included in this paper.

Description

Vertebral column

A syncervical, eighteen separate presacral vertebrae, and seven caudal vertebrae are preserved in CMN 344 (Figures 1–16). The incomplete presacral vertebral column of TMP 1989.097.001 comprises a syncervical, five other cervicals, and eight dorsal vertebrae (Figures 24–27). The caudal series of the latter specimen is complete and articulated (Figures 28–30).

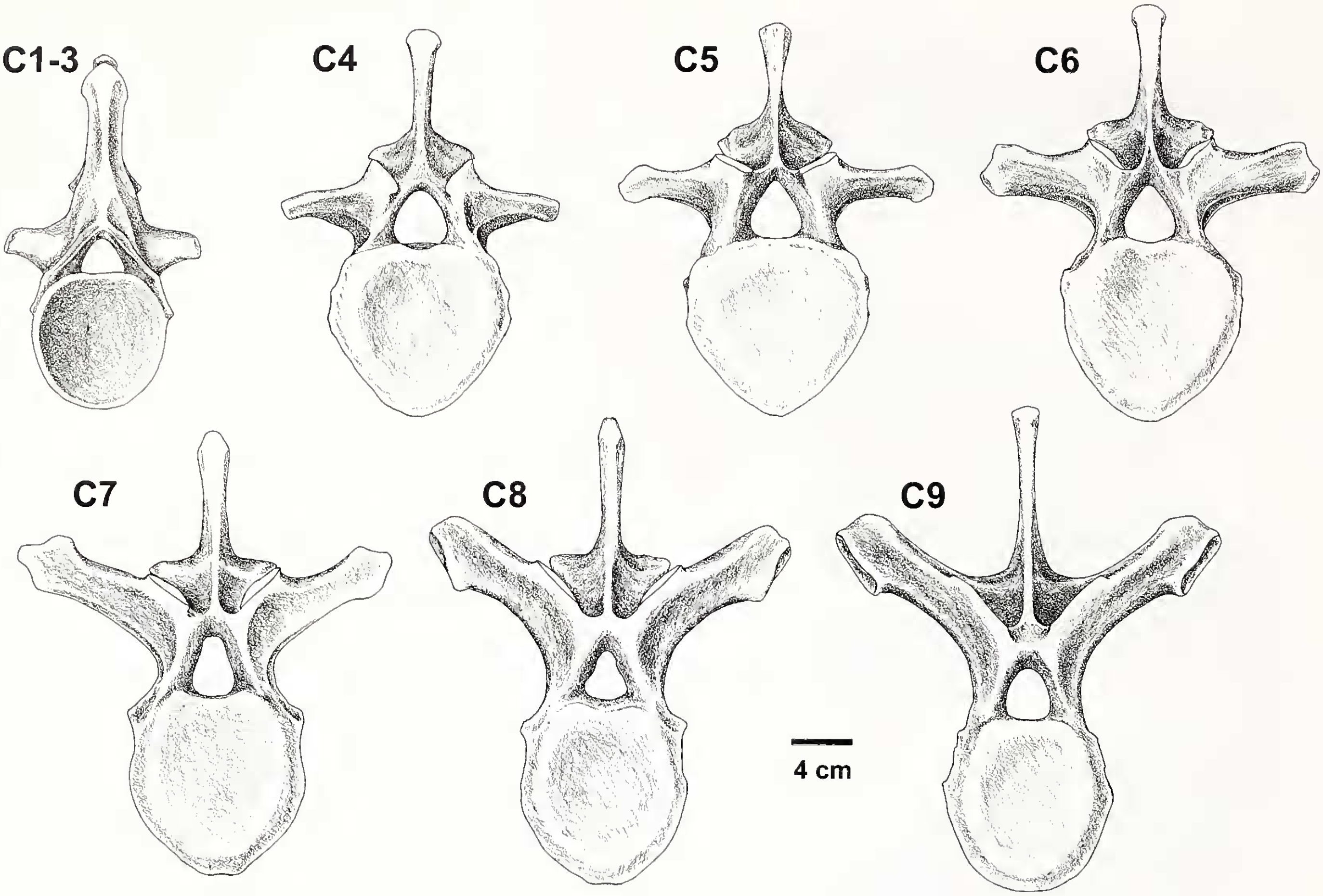

Figure 4. *Styracosaurus albertensis*, CMN 344. Cervical vertebrae (C1–C9) in anterior view. Scale bar equals 4 cm.

The presacral count of CMN 344 (nine cervical and 12 dorsal vertebrae), which matches that of *Centrosaurus* (Brown, 1917), is considered to be typical for ceratopsids (Dodson et al., 2004). In the original display mount, an additional vertebra, fabricated entirely in plaster, was inserted between the last cervical and first dorsal vertebrae. The reasons for this addition are uncertain, since there is no evidence that any presacral vertebrae are missing. However, C. M. Sternberg, who supervised the mounting of this specimen, may have used a well preserved, articulated postcranial skeleton (CMN 8547), usually attributed to the chasmosaurine *Anchiceratops*, as a guide. This skeleton is unusual in possessing supernumerary presacral vertebrae (Mallon and Holmes, 2010), and it is possible that this misled Sternberg into assuming that at least one presacral vertebra was missing from CMN 344.

As in other ceratopsids, the three anterior cervical vertebrae are co-ossified to form a syncervical (see Campione and Holmes, 2006; Tsuihiji and Makovicky, 2007). The anterior surface of the centrum of the syncervical bears a deep, circular cotyle to receive the occipital condyle. The posterior end of the syncervical bears an essentially flat, heart-shaped facet for articulation with the centrum of the first free cervical vertebra (Figures 2, 4–6). The most anterior (atlantal) neural arch is paired. Each half arises from the dorsal surface of the compound centrum at the midpoint of the first constriction and dorsally fuses indistinguishably with the lateral surface of the second, much more robust (axial) arch. No remnants of zygapophyses persist. There is no evidence of diapophyses or parapophyses to indicate the presence of an atlantal rib. A small, slit-like canal for passage of the spinal nerve separates the bases of these arches. Both the centra and zygapophyses of the second and third segments of the syncervical are co-ossified. Immediately ventral to these zygapophyses, a large circular nerve foramen pierces the bone. Each centrum bears a short parapophyseal process at mid-height. The tapered third neural spine, similar to those on more posterior cervical vertebrae, projects posterodorsally. Immediately ventral to the base of the short transverse process, the lateral wall of the arch of the third syncervical vertebra bears a deep pocket. Although superficially resembling a foramen, it does not pierce the laminar bone surface. A similar feature has been described on cervical vertebrae of *Chasmosaurus* (CMN 2245, NHMUK R4948 [Maidment and Barrett, 2011]) and *Vagaceratops* (CMN 41357, RH, pers. obs., August, 2012), but they apparently do not occur in all individuals, and when they do, the number of vertebrae showing the feature varies, and so their significance is uncertain.

The six vertebrae immediately posterior to the syncervical (Figures 2, 4–6) bear parapophyses on the lateral surfaces of their centra and are therefore considered here to be cervicals (see below). The first free cervical (C4) bears a parapophyseal facet at mid-height on the centrum. This facet becomes progressively more dorsal in position toward the posterior end of the cervical series, and in the last cervical (C9), occupies the anterolateral quadrant of the lateral surface of the centrum. The anterior facets

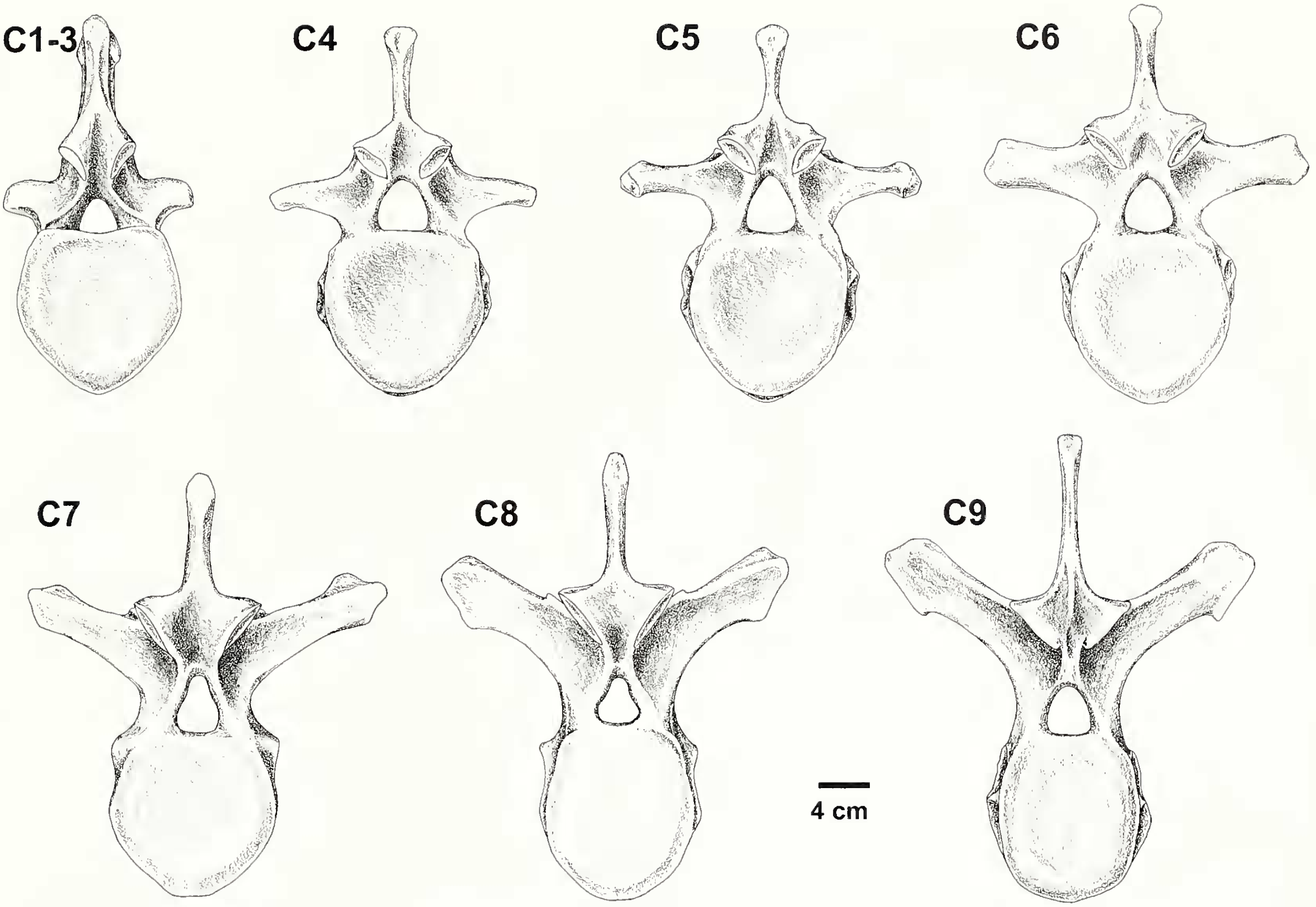

Figure 5. *Styracosaurus albertensis*, CMN 344. Cervical vertebrae (C1–C9) in posterior view. Scale bar equals 4 cm.

of the cervical centra are nearly flat, bearing only a lightly raised rim and very shallow central depression. The posterior facets are slightly more concave, but otherwise similar to the anterior facets. The centra of the more anterior cervicals are distinctly heart-shaped in outline, in contrast to the quasi-circular outline seen in the vertebrae of *Centrosaurus* (Lull, 1933) and *Triceratops* (Ostrom and Wellnhofer, 1986). Although the centra maintain approximately the same height throughout the cervical series, they become anteroposteriorly shorter, a trend also observed in *Centrosaurus* (Brown, 1917) and transversely narrower towards the posterior end of the series, with the anterior surfaces of the eighth and ninth cervicals presenting quasi-circular and dorsoventrally elongate oval outlines, respectively.

The neural arch pedicels of the last vertebral unit of the syncervical and first three free cervicals (i.e., C4–C6) each bears on its lateral surface a deep circular pit resembling those on the third vertebra of the syncervical. The distinctly triangular neural canals are large in comparison to those of the dorsal vertebrae, indicating that spinal tissue associated with the brachial plexus was accommodated in this part of the column (Giffen, 1995). The prezygapophyses of the first free cervical vertebra (C4) form a relatively steep angle of approximately 45° with the frontal plane, suggesting that axial rotation relative to the syncervical was restricted. However, its postzygapophyses form a much lower angle of about 25° with the frontal plane, matching closely the inclination of the prezygapophyses of the next (second free) cervical. This angle gradually increases toward the posterior end of the cervical region, reaching a maximum of about 50° in the most posterior (ninth) cervical. The articular surfaces of prezygapophyses of the cervical vertebrae are distinctly convex, and match closely with the complementary concave facets on the postzygapophyses. Although this configuration of the articular surfaces would have permitted lateral and dorsoventral flexion, it would have strongly resisted any axial rotation of the neck. In the first free cervical, the transverse processes are directed laterally and slightly ventrally, in contrast to the condition in *Triceratops* cervical vertebrae, in which they are directed dorsolaterally (Hatcher et al., 1907; Ostrom and Wellnhofer, 1986). However, in at least one specimen of *Chasmosaurus*, the orientation matches that of CMN 344 (Maidment and Barrett, 2011). Orientation of the transverse processes of this vertebra has not been described in centrosaurines, but published figures (Brown, 1917: plate xxxvii; Lull, 1933: fig. 8) suggest a lateral or slightly ventrolateral orientation. This process is directed laterally in the second free cervical, slightly dorsally in the third, and gradually attain a dorsolateral orientation in more posterior cervicals, forming an angle of about 40° with the frontal plane in the last (ninth) cervical, much as described for *Chasmosaurus* (Maidment and Barrett, 2011: fig. 17). The diapophyseal surfaces face laterally in the anterior vertebrae, but gradually become reoriented to face

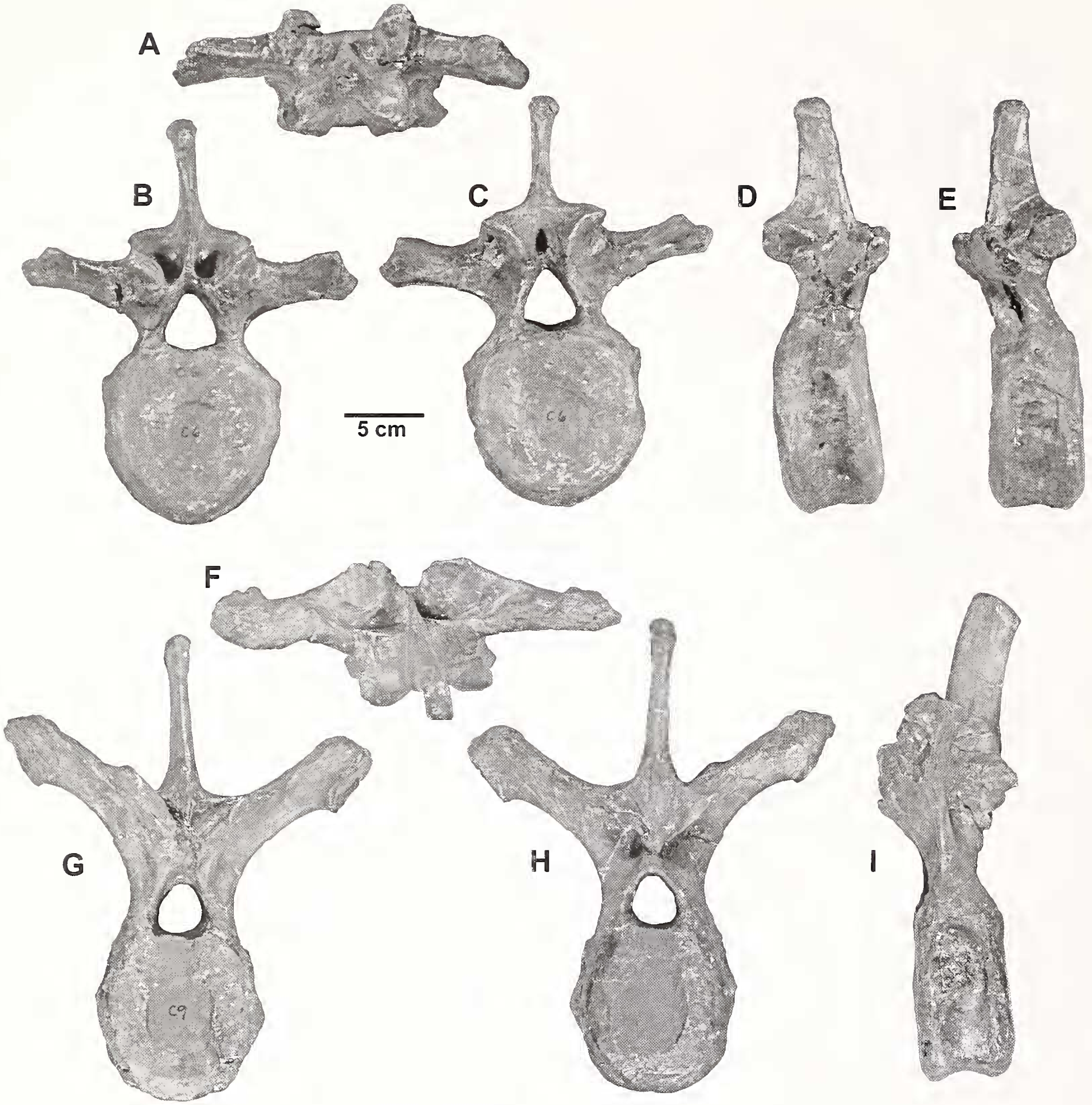

Figure 6. *Styracosaurus albertensis*, CMN 344, cervical vertebrae. Cervical vertebra 6 in, A, dorsal, B. anterior, C, posterior, D, right lateral, and E, left lateral views. Cervical vertebra 9 in F, dorsal, G. anterior, H, posterior, and I, left lateral views. Scale bar equals 5 cm.

ventrolaterally at the posterior end of the cervical series. The neural spines of C4 to C6 are approximately the same height, but from C7 to C9 they become progressively slightly longer. Anterior and posterior margins of the spines converge dorsally. Each spine flares at its dorsal tip to form a prominent knob that is thicker posteriorly than it is anteriorly. This morphology becomes less pronounced in the posterior part of the cervical series, where the spines gradually become more flattened, upright, and rectangular in outline.

The tenth vertebra is characterized by an abrupt shift of the parapophysis from the lateral surface of the centrum to the base of the neural arch (Figure 7). This is generally taken to mark the beginning of the dorsal series (e.g., Brown, 1917; Sternberg, 1951; Dodson et al., 2004; but see Ostrom and Wellnhofer, 1986 for an alternate interpretation). The centrum is slightly taller but narrower than that of the last cervical, appearing as a dorsally elongate oval in anterior view (Figure 8). The neural canal, although retaining its triangular outline, is distinctly smaller than in any cervical vertebra, indicating that the bulk of the brachial plexus exited the spinal cord anterior to this point (Giffen, 1995). The transverse processes are more elongate, and the diapophyseal surfaces face more laterally than in the last cervical vertebra. The

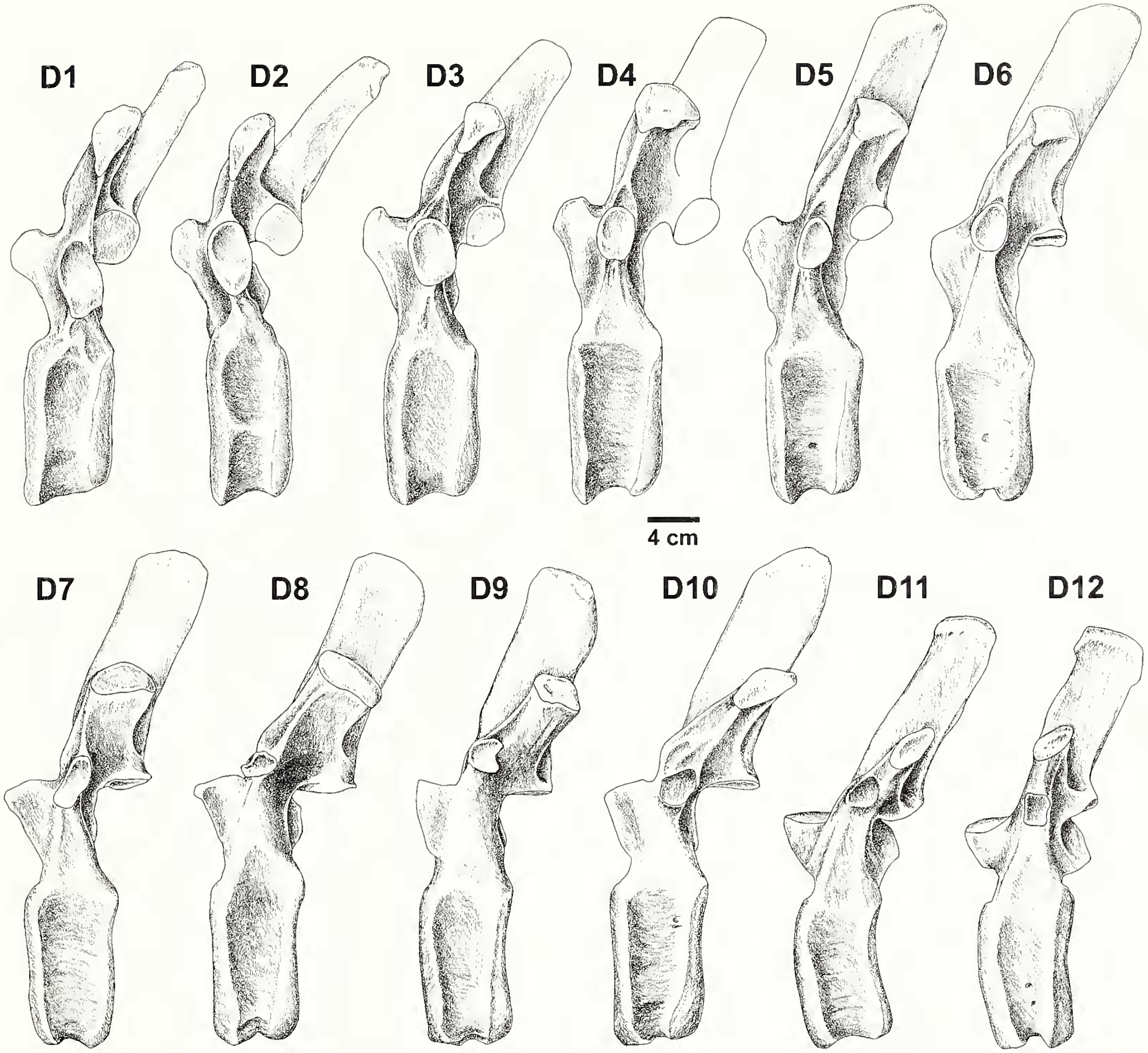

Figure 7. *Styracosaurus albertensis*, CMN 344. Dorsal vertebrae (D1–D12) in left lateral view. Scale bar equals 4 cm.

neural spines lean more posteriorly, but are otherwise similar to that of the last cervical vertebra.

The dorsal vertebral series (Figures 7–12) shows some clear anteroposterior trends. The centrum, exhibiting a dorsally elongate oval outline in the first four vertebrae, becomes slightly wider ventrally in the fifth dorsal vertebra and becomes slightly pear-shaped towards the posterior end of the series. A similar trend occurs in *Triceratops* (Hatcher et al., 1907; Ostrom and Wellnhofer, 1986), but not in *Centrosaurus*, in which the dorsal centra are more circular in outline throughout the column (Lull, 1933). The zygapophyses, sharply angled (45° to the frontal plane) in the first dorsal vertebra, gradually rotate to a more horizontal orientation (about 25° in the last dorsal vertebra). Prezygapophyses become larger, approaching the midline, and in the seventh dorsal vertebra, fuse to form a single dorsally-facing concave articular surface (Figure 9), although a remnant of the cleft is variably retained on the anterior surface of the conjoined prezygapophyses. This cleft reopens in the last (12th) dorsal vertebra. It has been suggested (Maidment and Barrett, 2011) that this median fusion of zygapophyses is an ontogenetic feature, presumably only occurring in older individuals. Articular facets of the prezygapophyses of the posterior dorsal vertebrae vary from a gentle cup shape (dorsal vertebrae 7, 8, 10) to gently convex (dorsal vertebrae 9, 11, 12). In most of the dorsal vertebrae (probably all, but preservation is not good enough to be sure), the pedicels of the postzygapophyses fuse to form a sharp, median, posteriorly projecting keel (Figures 10–12). The keel of the 11th dorsal vertebra is particularly well developed, and extends posteriorly to insert into deep slots between the prezygapophyses of the 12th dorsal vertebra. An equally prominent keel on the 12th

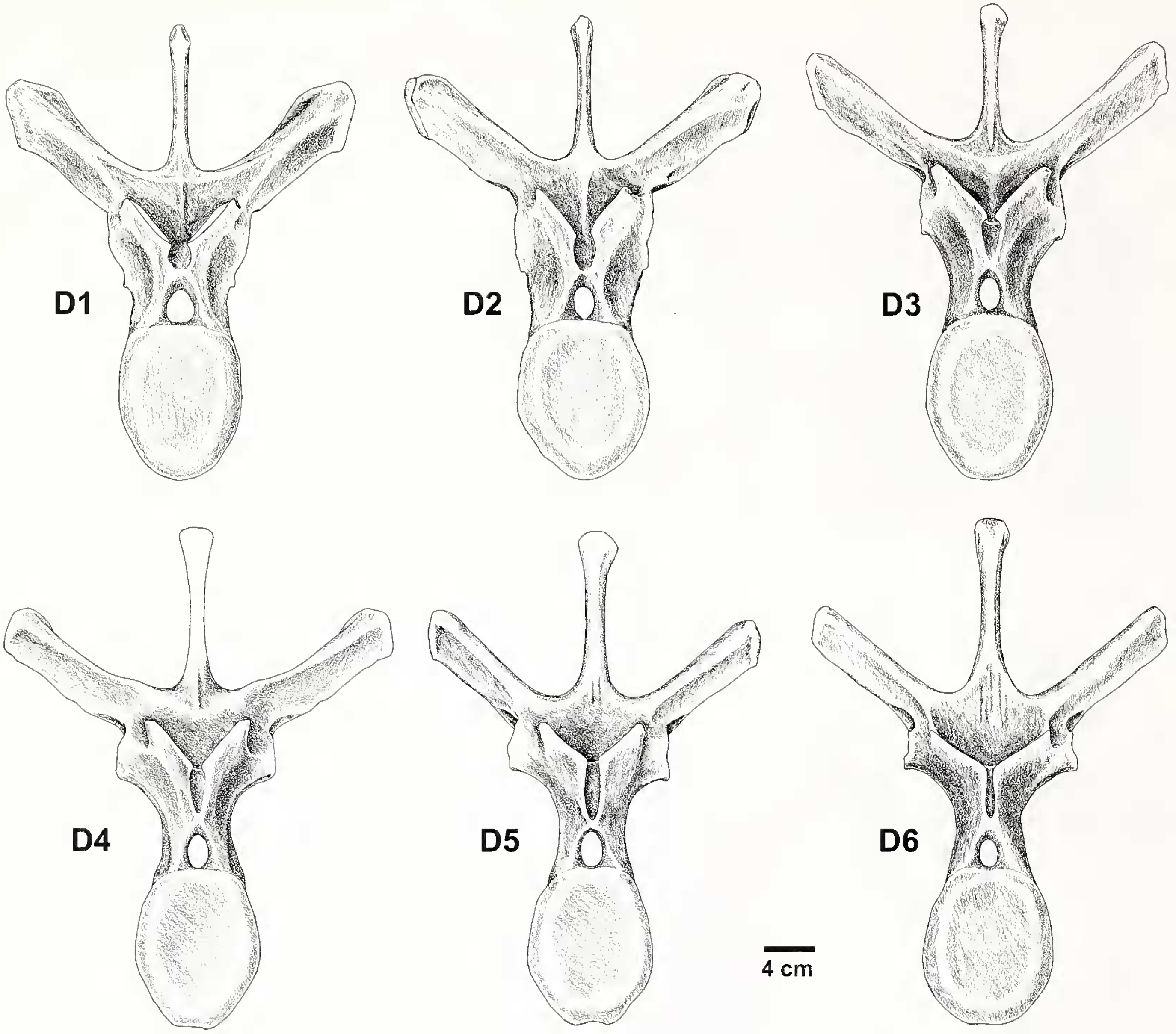

Figure 8. *Styracosaurus albertensis*, CMN 344. Dorsal vertebrae (D1–D6) in anterior view. Scale bar equals 4 cm.

dorsal vertebra presumably inserted between the prezygapophyses of the first dorsosacral vertebra, although the latter is not preserved. The postzygapophyses of the 12th dorsal vertebra face posteriorly as well as dorsally.

The parapophyseal facet is borne on the lateral surface of the neural arch pedicel on the first few dorsal vertebrae. It gradually migrates dorsolaterally onto the ventral surface of the transverse process in more posterior vertebrae, and in the last few dorsal vertebrae is located at least one-third of the distance between the base and tip of the process. This facet is largest in the anterior dorsal vertebrae, and becomes smaller toward the posterior end of the dorsal series, reflecting the reduced size of the capitulum of the posterior ribs. Neural spines become both taller and anteroposteriorly broader until about the fifth or sixth dorsal. These proportions are maintained to the 10th dorsal vertebra, after which there is a modest decrease in dimensions. Although the neural canal of the first dorsal vertebra is triangular in outline, in all subsequent dorsals, it is oval. Although variable in size, it appears to be smallest at or near the middle of the dorsal series. There is no evidence that the 12th dorsal vertebra had begun to fuse to the sacrum. In this, it resembles Brown's (1917) *Centrosaurus* specimen, but not Lull's (1933) specimen, in which the 12th dorsal has fused to the front of the sacrum to become a dorsosacral. However, it is clear that the latter vertebra is homologous to the last (12th) dorsal vertebra of CMN 344, as its associated ribs (Lull, 1933, fig. 18) closely resemble those associated with the 12th dorsal vertebra of CMN 344, and the 11th dorsal vertebra of Lull's specimen (Lull, 1933, fig 16) is very similar to the 11th dorsal vertebra of CMN 344. Lull's specimen has a second dorsosacral vertebra that lacks ribs. Its distally expanded diapophyses fuse to the ilium. This morphology is not present in the most posterior dorsal vertebrae of CMN 344.

Seven caudal vertebrae (Figures 13–16) are preserved in CMN 344. The two largest, lacking facets for reception of chevrons,

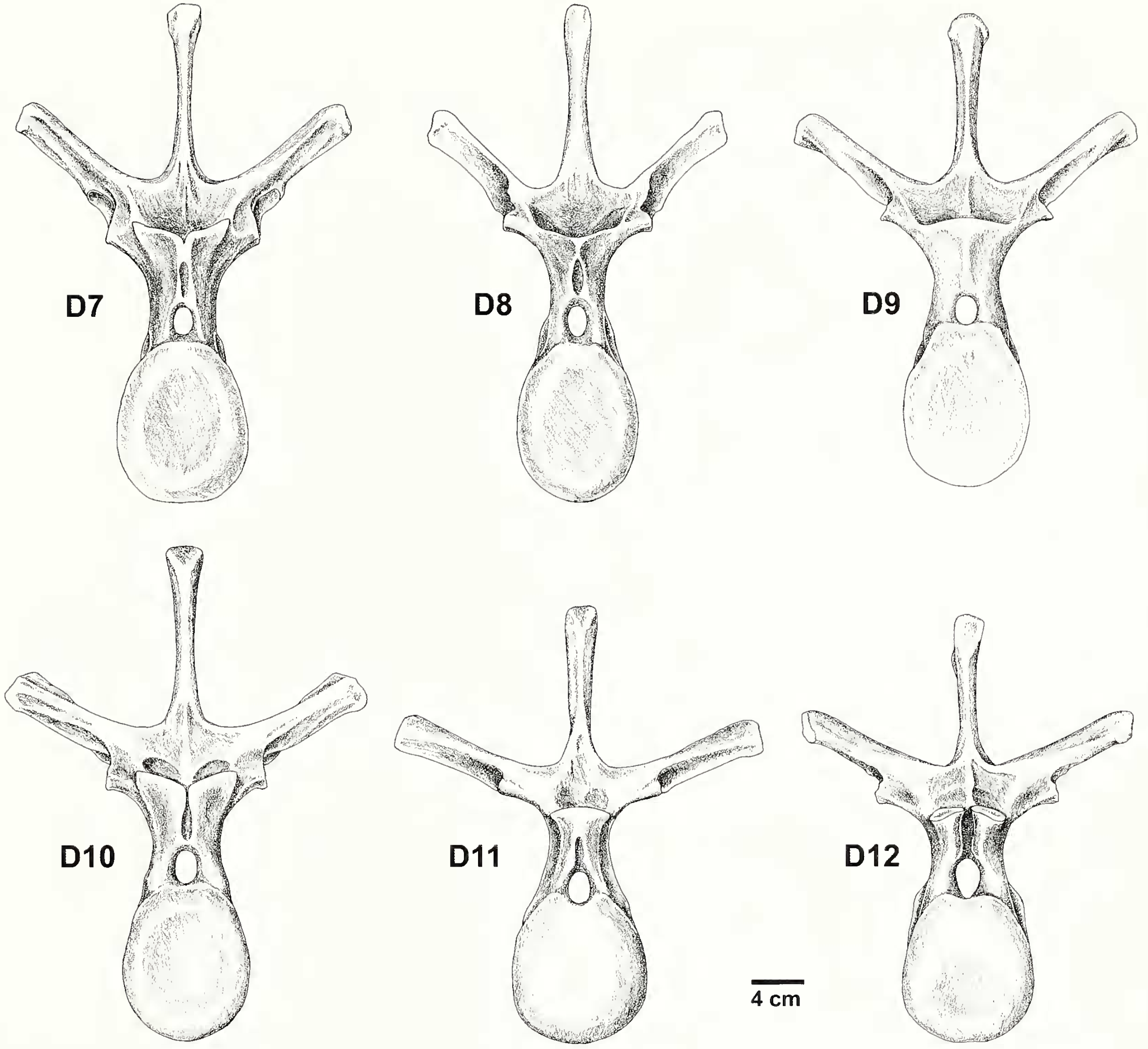

Figure 9. *Styracosaurus albertensis*, CMN 344. Dorsal vertebrae (D7–D12) in anterior view. Scale bar equals 4 cm.

probably represent the first and second caudal vertebrae. Their transverse processes project anteriorly as well as laterally. A third vertebra, extensively restored in plaster (see Holmes et al., 2005, plate 10), was inserted immediately behind the second in the original mount. Since its true morphology cannot be established, it will not be described or illustrated here. All of the remaining vertebrae bear facets for chevrons. In *Centrosaurus* and cf. *Anchiceratops* (CMN 8547), the first chevron articulated between the third and fourth caudal vertebrae (Brown, 1917; Mallon and Holmes, 2010), suggesting that no vertebrae are missing from the preserved series described here. All are approximately the same size and exhibit similar morphology, and can be assembled into a series that plausibly represents the fourth to eighth caudals. Viewed laterally, the centra of most of the caudal vertebrae are slightly longer dorsally than ventrally, forcing the base of the tail to a distinct ventral curvature, much as observed in *Triceratops* (Larson and Ott, 2004).

A complete tail is preserved in articulation with the sacrum in TMP 1989.097.001. As much matrix as practical was removed from the 17 proximal caudal vertebrae, but otherwise they were left in articulation as preserved (Figure 28). The 28 distal caudal vertebrae have been removed from the matrix, and many of them have been separated (Figure 29). The angle of articulation of the proximal caudal vertebrae confirms the observation, based on the partial tail of CMN 344 that the tail curved ventrally immediately posterior to the sacrum.

Of the 45 caudal vertebrae, only the first 20 bear transverse processes, as compared with 25 in *Brachyceratops* (Gilmore, 1917), 23 in *Centrosaurus* (Brown, 1917), 22 in cf. *Anchiceratops* (Mallon and Holmes, 2010), and 19 in *Pentaceratops* (Wiman,

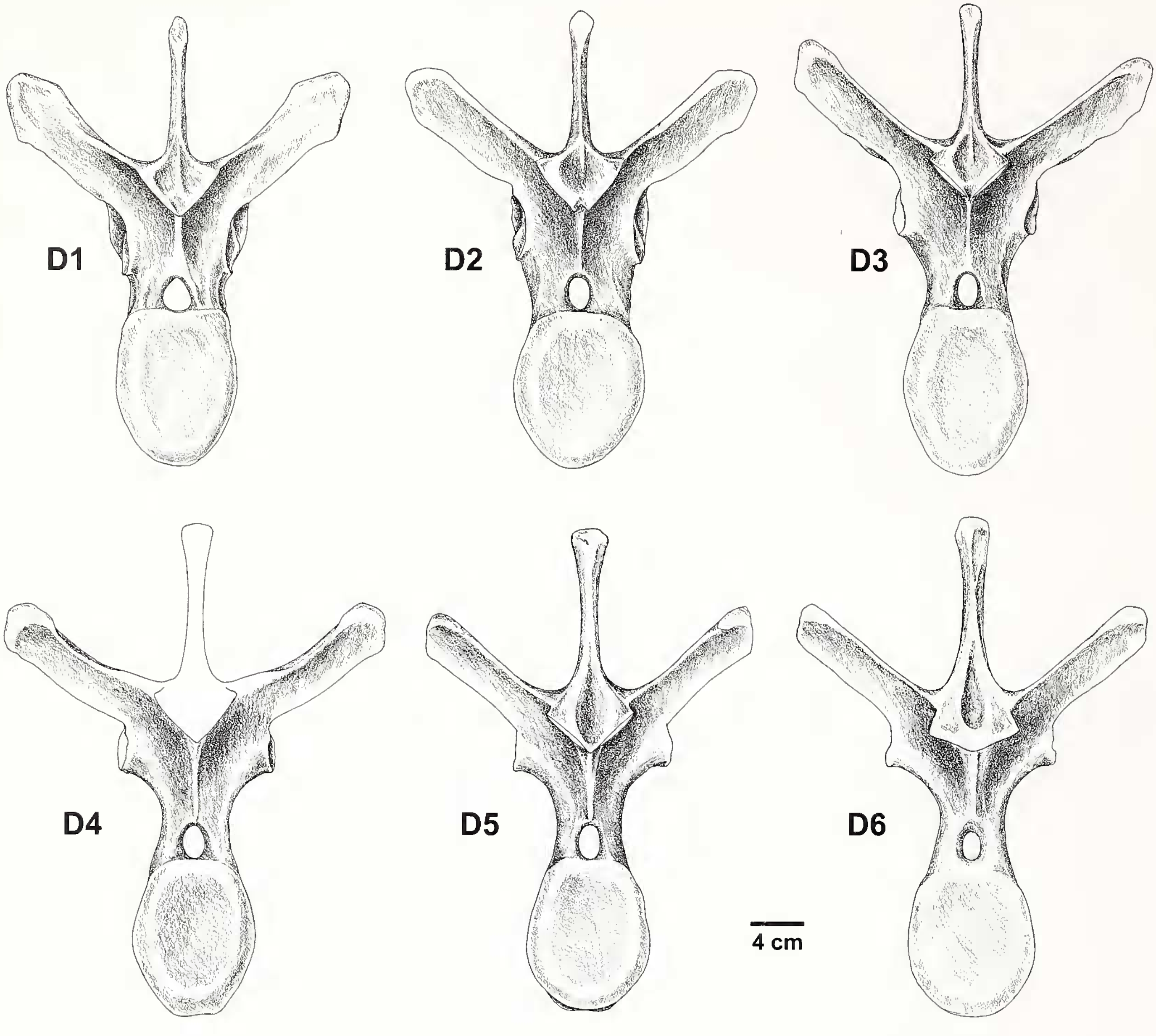

Figure 10. *Styracosaurus albertensis*, CMN 344. Dorsal vertebrae (D1–D6) in posterior view. Scale bar equals 4 cm.

1930). The transverse processes of the first three caudal vertebrae are incomplete. However, it is clear that the process of the first caudal vertebra is directed strongly anteriorly, that of the second, anterolaterally, and that of the third, directly laterally, as are those of all more posterior caudal vertebrae. A similar trend is also seen in CMN 344, although the anterior deflection of the transverse processes of the first caudal vertebra is not as pronounced. Although the processes gradually diminish in size anteroposteriorly, their disappearance in the 21st caudal is abrupt (Figure 30). Four vertebrae (27–30) are pathological—extensive co-ossification has occurred, and their anatomy has been obscured by considerable secondary bone growth (Figure 29). Although well developed prezygapophyseal processes are present as far posteriorly as the 36th caudal, the most posterior postzygapophyseal processes appear to occur between the 26th and 27th caudal (or possibly between 27 and 28—secondary bone growth in the pathological section of the tail makes it difficult to tell). This indicates that the last several prezygapophyseal processes were not functional (Figure 30). The most posterior neural arches are not preserved, but broken stumps indicate that they were present on all caudals except the last two (44 and 45). These latter vertebrae, each about half of the length of the 43rd caudal, are co-ossified, although the separation between the two elements is clearly marked by a raised ridge on the ventral and lateral surfaces of the compound element.

The most anterior preserved chevron is located between caudal vertebrae four and five, although there may have been one between caudals three and four—the ventral aspects of the centra are not well enough exposed to confirm the presence of facets for its reception. Chevrons are preserved as far posteriorly as the 17th caudal. Although their distal ends are not generally well preserved, there appears to be little or no lateral compression or

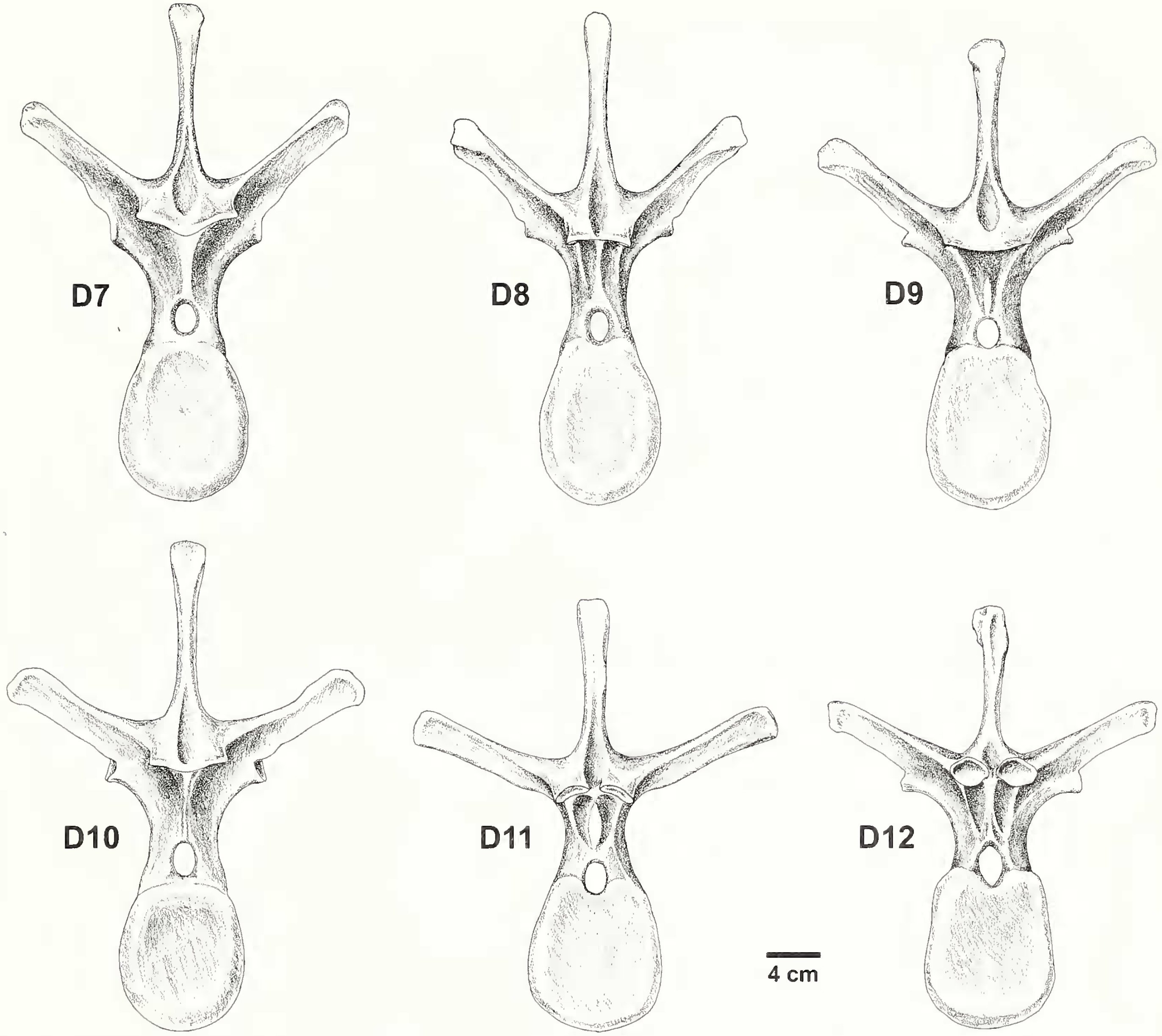

Figure 11. *Styracosaurus albertensis*, CMN 344. Dorsal vertebrae (D7–D12) in posterior view. Scale bar equals 4 cm.

anteroposterior expansion to form a blade. Bevels preserved on the ventral rims of the centra indicate that chevrons were present as far back as caudal vertebra 32.

The total count of 45 caudal vertebrae compares closely with that of other centrosaurines with complete tails; *Centrosaurus* has 46 (Brown, 1917), and *Brachyceratops*, 47 (Gilmore, 1917); but this number is distinctly higher than in chasmosaurines in which the count can be established or estimated: 39 in *Anchiceratops* (Mallon and Holmes, 2010), at least 30 in *Pentaceratops* (Wiman, 1930), and approximately 40 in *Chasmosaurus*—(CMN 2245, RH, pers. obs., August, 2012).

Sacrum

The synsacrum is not preserved in CMN 344, and although present in TMP 1989.097.001, it is obscured by the right ilium and ossified tendons (Figure 24). However, a partial synsacrum is preserved in TMP 2009.080.001. Co-ossification is advanced, but there appear to be two dorsosacral vertebrae present, as the portion of the sacral bar immediately anterior to the first sacral vertebra is nearly twice as long as the first sacral centrum (Figure 31). As in *Triceratops* (Hatcher et al., 1907) and *Chasmosaurus* (Maidment and Barrett, 2011), the broad base of the large first sacral rib originates from the posterolateral part of the second dorsosacral as well as from the lateral surface of the centrum of the first sacral vertebra. The midventral surface of the first two sacral vertebrae and anterior half of the third bear a shallow, indistinct longitudinal groove (Figure 31). The ventral surfaces of the fourth sacral and the first two preserved caudosacrals actually bear a low midventral keel. Maidment and Barrett (2011) have suggested that a midventral, longitudinal

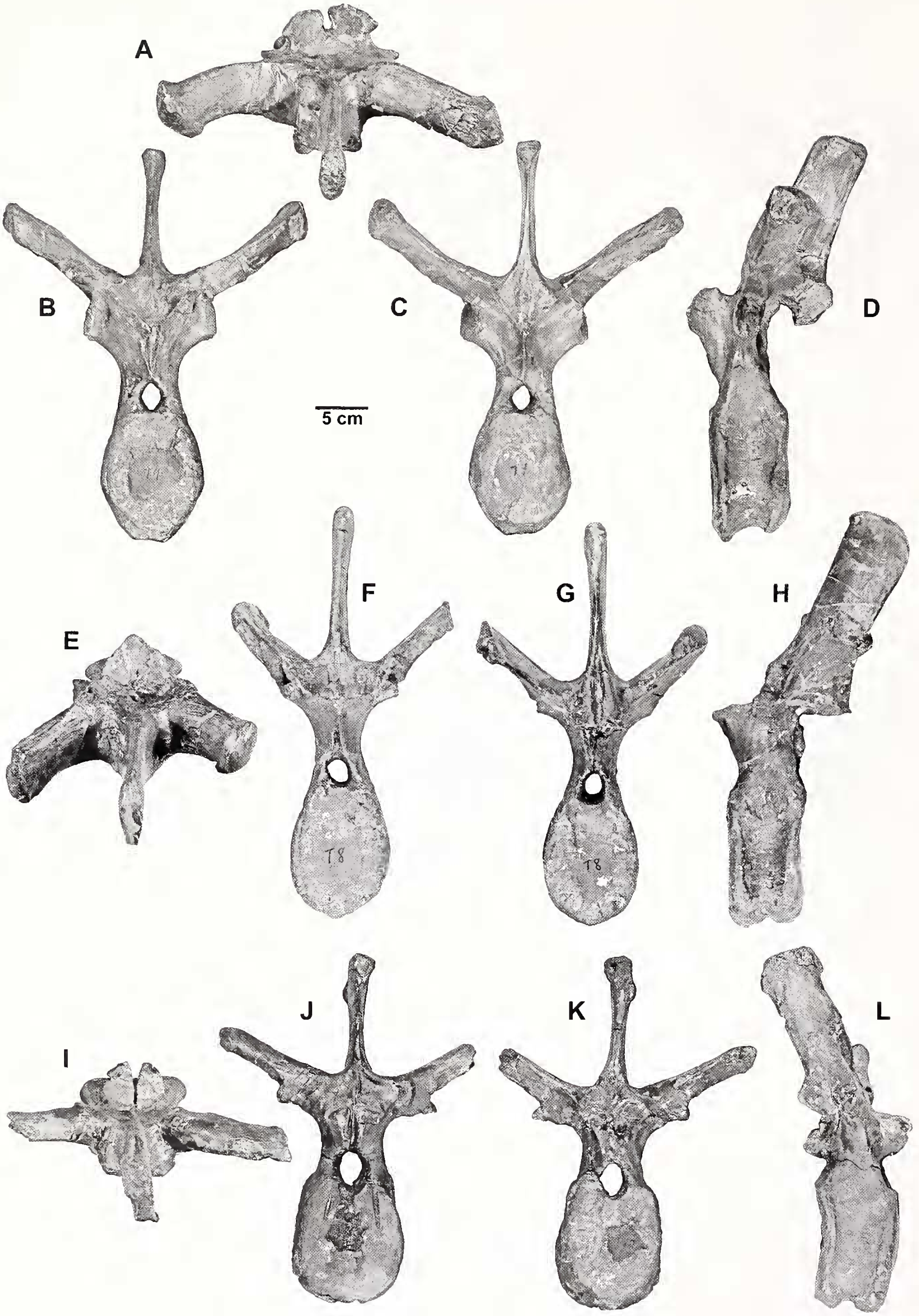

Figure 12. *Styracosaurus albertensis*, CMN 344, dorsal vertebrae. Dorsal vertebra 4 in A, dorsal, B, anterior, C, posterior, and D, left lateral views. Dorsal vertebra 8 in E, dorsal, F. anterior, G, posterior, and H, left lateral views. Dorsal vertebra 12 in I, dorsal, J, anterior, K, posterior, and L, right lateral views. Scale bar equals 5 cm.

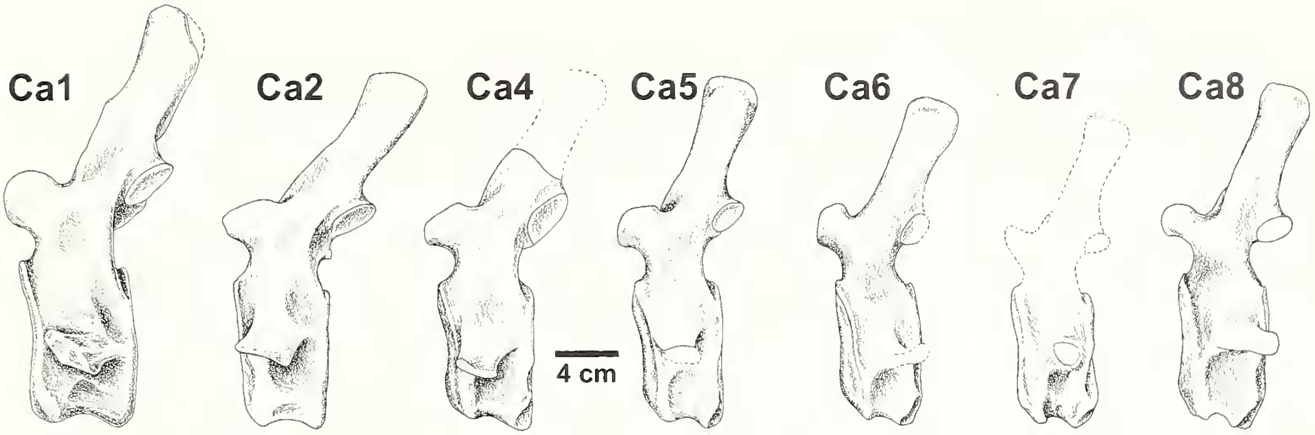

Figure 13. *Styracosaurus albertensis* CMN 344. Caudal vertebrae (1, 2, 4–8) in left lateral view. Scale bar equals 4 cm.

groove, present in the sacrum of all ceratopsids, is conspicuous in chasmosaurines, but is poorly developed in centrosaurines. This specimen supports their hypothesis.

Ribs (Holmes et al., 2005, plates 13–19; Figures 17, 24, 25, 32, and 33 of this paper)

The ribcage of CMN 344 is largely complete (see Holmes et al., 2005 for details). Several ribs, disarticulated from their vertebrae, are preserved in TMP 1989.097.001. As in other ceratopsids, the atlantal segment of the syncervical lacks ribs. The axial segments bear diapophyses and parapopophyses, but neither axial rib is preserved. The rib associated with the last syncervical segment (third cervical) comprises a broad, flat lamina connecting the dorsal tuberculum and ventral capitulum, and a short shaft. As in *Centrosaurus* (Brown, 1917), a short triangular spine projects from the anterior edge of this lamina. A distinct neck is lacking. The flattened, laterally convex shaft of the next rib (associated with the first free, or fourth, cervical vertebra) expands distally to form a rounded crest dorsally and a longer, triangular spine ventrally. The rib associated with the fifth cervical vertebra is similar to that of the fourth, although the ventral spine-like process of the shaft turns gently laterally toward its tip. This effect is more pronounced in the sixth rib, which is otherwise very similar to the fifth.

The tuberculum and capitulum become more widely separated in more posterior cervical ribs as the connecting lamina becomes progressively reduced. All ribs turn sharply ventrally at their necks, so that their straight shafts project directly posteroven-

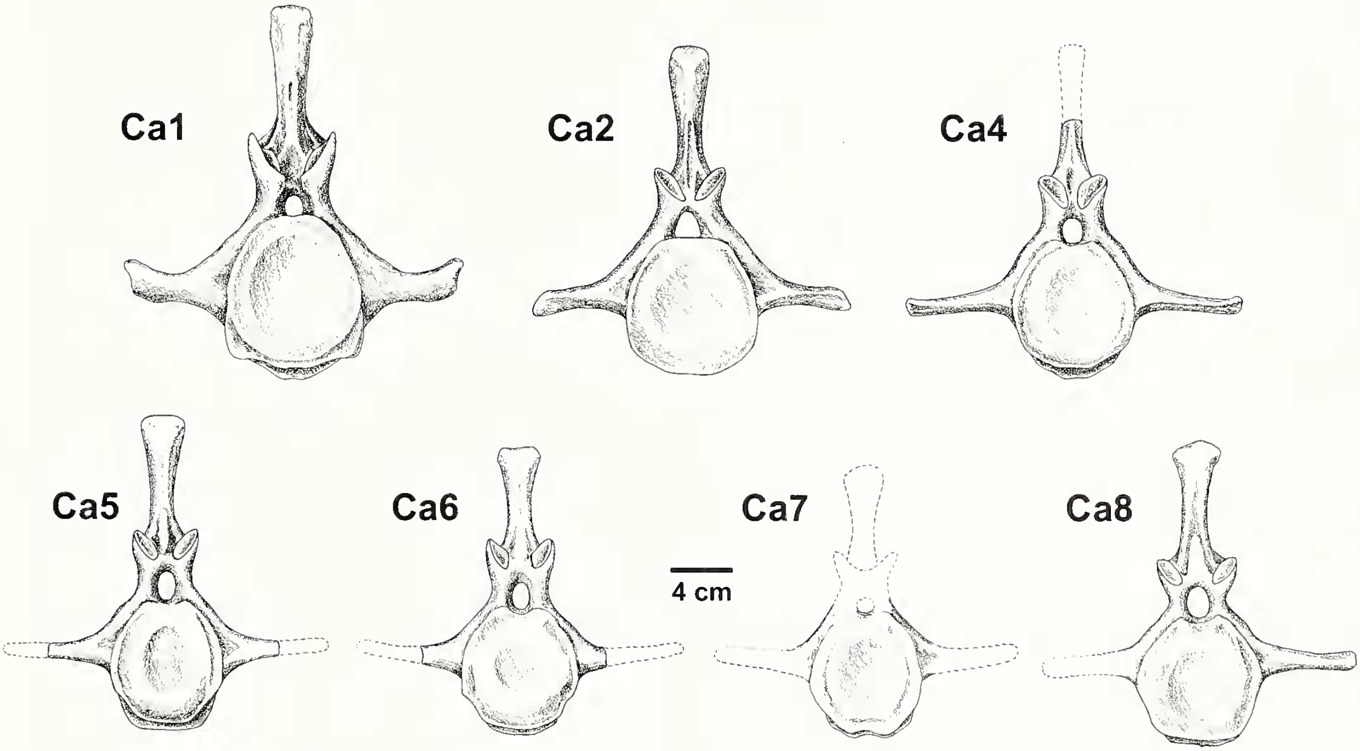

Figure 14. *Styracosaurus albertensis* CMN 344. Caudal vertebrae (1, 2, 4–8) in anterior view. Scale bar equals 4 cm.

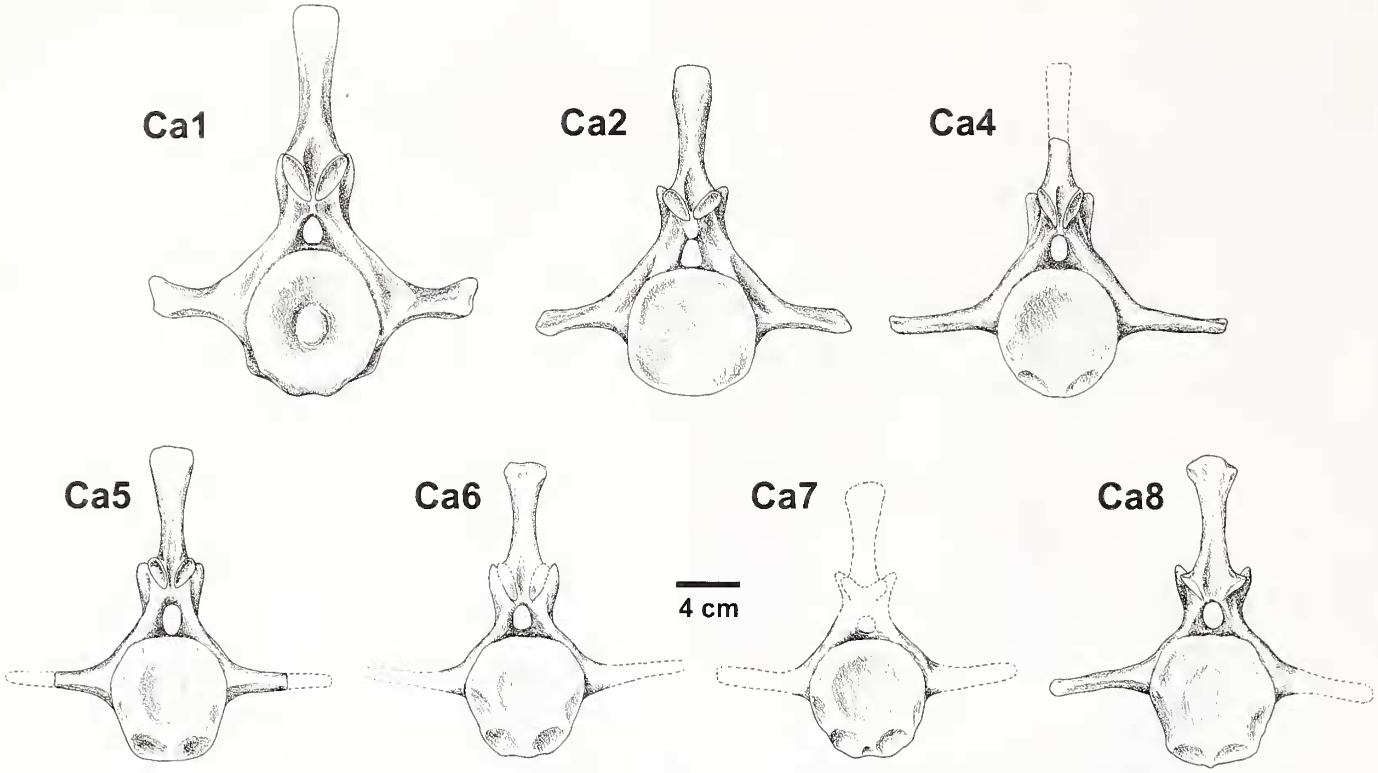

Figure 15. *Styracosaurus albertensis* CMN 344. Caudal vertebrae (1, 2, 4–8) in posterior view. Scale bar equals 4 cm.

trally. The shafts become longer toward the posterior end of the series. The ribs associated with the second, third and fourth free cervical vertebrae (i.e., C5 to C8) attenuate to a point ventrally, indicating a lack of cartilaginous costal extensions. However, the end of the last cervical rib expands both anteroposteriorly and mediolaterally, suggesting that it may have continued in cartilage to the sternum.

The rib associated with the first dorsal vertebra is distinct from that of the last cervical in having a much shorter capitular shaft that correlates with the abrupt dorsal migration of the parapophysis from the centrum of the vertebra to the lateral surface of the neural arch pedicel. Both capitular and tubercular shafts are extremely broad and spatulate. Its slightly flattened shaft, the most massive of the whole presacral series, is distinctly more curved than any of the cervical vertebrae ribs, although the more distal portion of the shaft is almost straight. Its expanded, rugose termination indicates continuation in cartilage.

A number of trends are apparent in the thoracic rib series. The tubercular shaft becomes further reduced posterior to the first thoracic rib, and by the fourth thoracic, it is essentially absent. In more posterior thoracic ribs, the tubercular facet occupies a triangular notch on the dorsal surface of the angle of the rib. Both tubercula and capitula become less massive, with the shape of their articular facets gradually changing from an elongate, flattened oval to quasi-circular in outline. The shaft of the first thoracic rib is essentially straight distal to the angle, but the more posterior ribs gradually develop more curvature. Beginning at the seventh thoracic rib, the shaft begins to twist relative to the plane of the proximal articulations, causing the rib to curve posteriorly as well as ventrolaterally. This trend continues until the 11th thoracic rib, in which the shaft forms a tight, posteroventromedial arc. On the inside of this arc, the rib shaft bears a flattened facet that may have provided articulation with the anterior margin of the prepubic process, as suggested by Sternberg (1927) for *Chasmosaurus*. The 12th thoracic rib, in contrast, is much shorter, essentially straight, and projects laterally and slightly anteriorly. A very similar rib, associated with the first dorsosacral (12th postcervical) has been described in *Centrosaurus* (Lull 1933, fig. 18). It articulates with (but does not fuse to) the parapophysis of the vertebra, and lies along the internal surface of the anterior iliac process.

The stout shafts of the second and third thoracic ribs, as in the first, are oval in cross section and are expanded it their distal ends for articulation with sternal ribs. However, more posterior thoracic ribs gradually become more flattened, and their rounded, spatulate ends show no evidence of cartilaginous extensions. None of the thoracic ribs bear facets to accommodate the scapula like those observed in *Triceratops* (Kozisek and Derstler, 2004; Larson and Ott, 2004).

Although many of the ribs show considerable distortion, a sufficient number have retained their original shape, allowing the ribcage to be reconstructed with considerable confidence (Figures 32 and 33). In general, the inferred body cross-section resembles that reconstructed by Lehman (1989) for *Agujaceratops* (*Chasmosaurus*) *mariscalensis*. Anteriorly, the chest is narrow but dorsoventrally deep, comprising relatively straight, ventrally directed rib shafts that are swept back at an angle of about 35° from the vertical. Only the first three thoracic ribs are expanded distally. All others taper distally, providing no evidence for presence of costal cartilages. Therefore, even if the last pair of cervical ribs is included, there is evidence for no more than four pairs of 'true' ribs that connected to the sternum. Brown (1917)

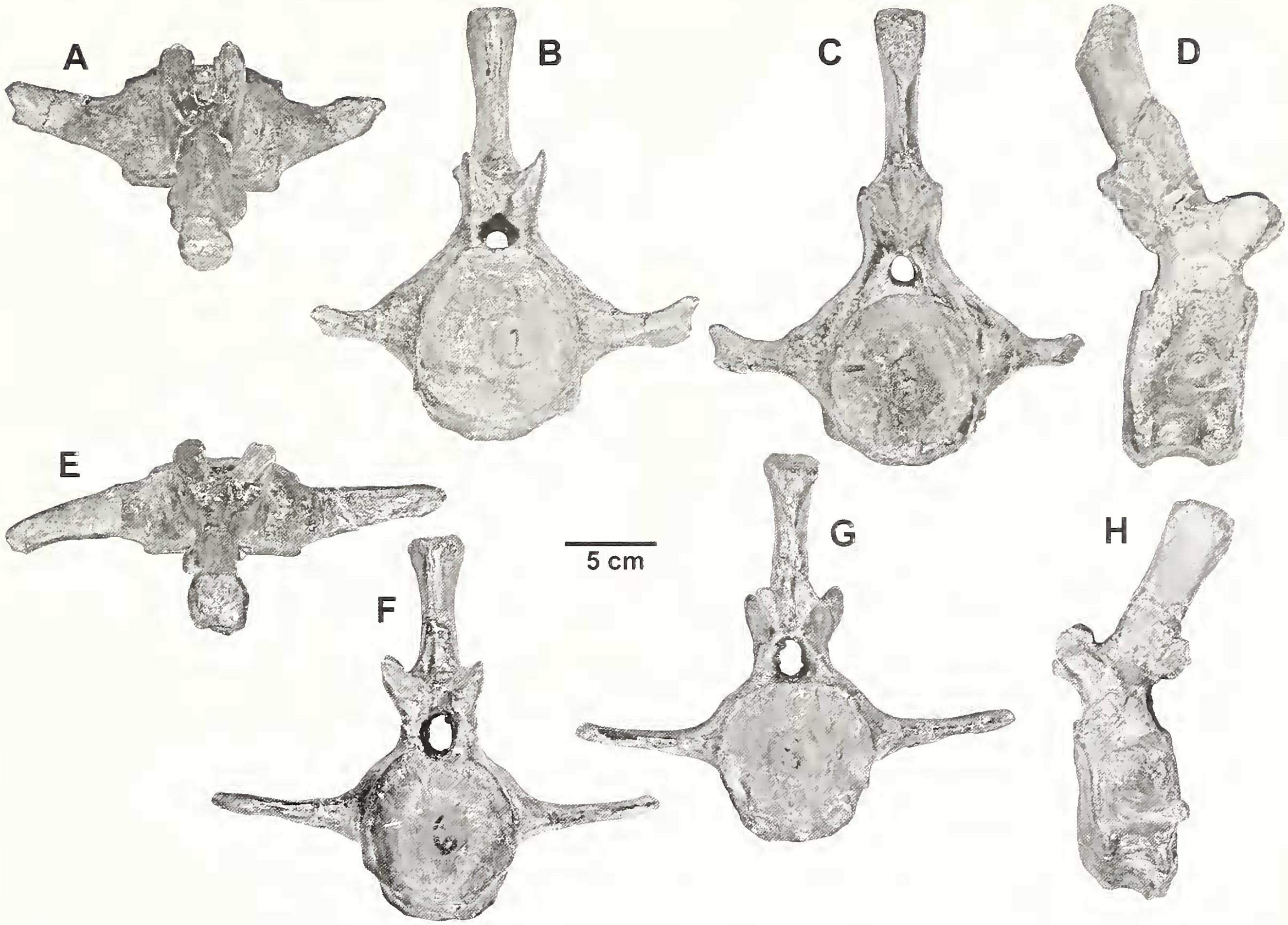

Figure 16. *Styracosaurus albertensis*, CMN 344, caudal vertebrae. Caudal vertebra 1 in A, dorsal, B, anterior, C, posterior, and D, right lateral views. Caudal vertebra 6 in, E, dorsal, F, anterior, G, posterior, and H, left lateral views. Scale bar equals 5 cm.

hypothesized the presence of up to 11 pairs of 'true' ribs in *Centrosaurus* based on what he took to be scars for individual costal cartilages on the posterior margin of the sternal plate. However, we have never observed distinct costal cartilage scars on any ceratopsid sternal plate, so cannot confirm such a high rib count. Ribs become longer until the fourth thoracic, then become shorter again, at first gradually, and then more rapidly after the 10th thoracic. Posteriorly, the rib shafts become more broadly curved and vertically oriented. Beginning at about the ninth thoracic, their necks arch dorsolaterally from the diapophyseal–capitular articulation, thus raising the dorsal wall of the body cavity, before turning laterally and then ventrolaterally to form a broad, but dorsoventrally shallow posterior thorax. The elevated ventral wall of the abdomen suggested by the shape of these ribs presumably accommodated anterior excursion of the hind limb.

Pectoral girdle and limb

Both scapulae, the right coracoid, and the right sternal plate are well preserved in CMN 344 (figure 18f; Holmes et al. 2005, plates 20–22). Only the right scapulocoracoid and humerus, and partial left scapulocoracoid and humerus are preserved in TMP 1989.097.001 (Figures 24, 25, 34). The coracoid is pierced on its lateral surface by a conspicuous coracoid foramen. Medially, the foramen opens into a distinct groove that leads to its common suture with the scapula (Holmes et al., 2005, plate 20). The supracoracoideus scar is not conspicuously developed. The prominent, laterally turning acromial process of the scapula is restricted to a short portion of the anterior scapular margin immediately distal to its suture with the coracoid (Figure 18; Holmes et al., 2005, plate 20).

Both humeri of CMN 344 are somewhat crushed, but complete (Figure 19; Holmes et al., 2005, plate 23). The dorsally arched, deltopectoral crest is much less extensive proximally than in most chasmosaurs (e.g., CMN 2280, ROM 843 [RH, pers. obs., August, 2012], NHMUK R4948, *Triceratops* [Hatcher et al. 1907, figs. 65–66]), and the insertional area for the pectoralis is less extensive and does not extend as far distally. Both ulnae and radii are preserved (Figure 20; Holmes et al., 2005, plates 24 and 25). As in other ceratopsids, the epipodium is distinctly shorter than the propodium, with the radius being about 65% of the length of the humerus. Only four distal elements can be accounted for: the first metacarpal of the right forelimb, and fourth metacarpal, and first and second distal phalanges of the left forelimb (Holmes et al., 2005, plate 30).

In contrast to the condition seen in *Triceratops* (Kozisek and Derstler, 2004; Larson et al., 2004), the ribs lack facets on their lateral surfaces to accommodate the scapular blade. As a consequence, it is impossible to position the scapula precisely, although its gently curvature conforms best to the relatively

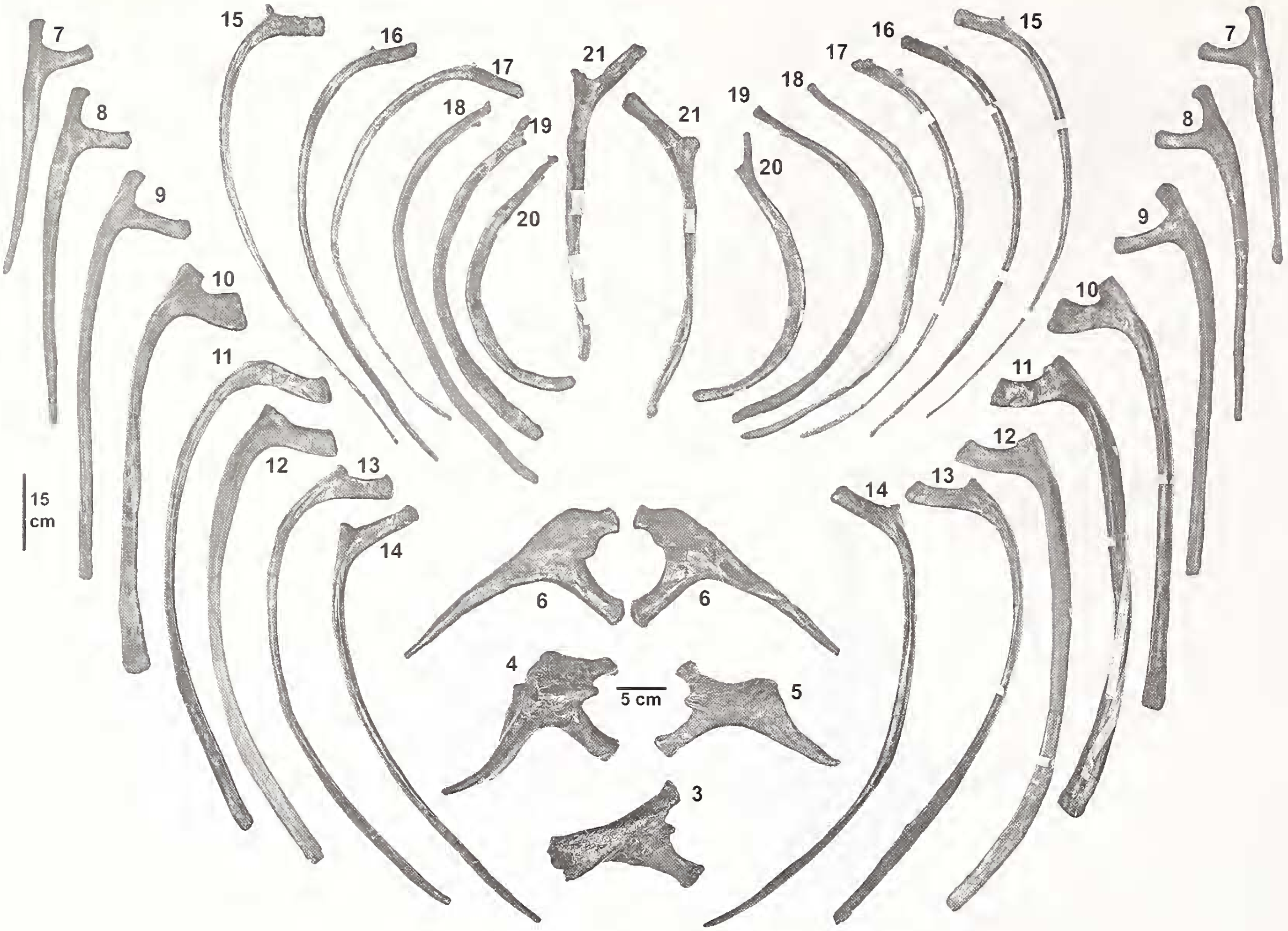

Figure 17. *Styracosaurus albertensis*, CMN 344, ribs in anterior view. 3–9, ribs associated with cervicals 3–9; 10–21, ribs associated with thoracic vertebrae 10–21. Scale bar for ribs 3–6 equals 5 cm. Scale bar for ribs 7–21 equals 15 cm.

straight ribs of the anterior-most thoracic region (Figure 1). With the scapulocoracoid in this position, the articulated humerus projects posterolaterally at an angle of about 30° parasagittally and slightly ventrally, much as hypothesized for other ceratopsids by Dodson and Farlow (1997) and as reconstructed for *Vagaceratops* (*Chasmosaurus*) *irvinensis* (Thompson and Holmes, 2007).

Pelvic girdle and rear limb

Of the pelvic girdle, only the right ilium and right and left ischia (Figure 21; Holmes et al., 2005, plates 26 and 27) are preserved in CMN 344. The entire right half, and much of the left half, of the pelvis is exposed in TMP 1989.097.001 (Figure 24). The anterior (preacetabular) blade of the right ilium is depressed and rotated so that its dorsal surface faces slightly laterally, and its gently curved posterior blade is rotated so that its ventrolateral surface faces essentially laterally. Otherwise, the proportions of the bone resemble those of the type as well as those described for the ilia of *Centrosaurus* (Brown, 1917) and cf. *Anchiceratops* (Mallon and Holmes, 2010).

The gently curved ischia resembles those of other centrosaurines (Brown, 1917; Gilmore, 1917; Lull, 1933), and protoceratopsids (Brown and Schlaikjer, 1940, 1942; You and Dodson, 2004), more than the distinctly strongly curved ischia seen in chasmosaurines (e.g., Hatcher et al., 1907, fig. 60; Wiman, 1930:plate 4; Lehman, 1989, fig. 19; Mallon and Holmes, 2010). Although the posterior process of the right pubis could not be identified in TMP 1989.097.001, the prepubic process is complete, and appears to be in its natural position. It projects almost directly anteriorly, much as in Dodson et al. (2004, fig. 23.5) rather than anteroventrally, as sometimes depicted (e.g., Brown, 1917, plate XIII), and its hatchet-shaped anterior end appears to articulate with the curved shaft of a posterior thoracic rib, probably that associated with the 11th dorsal vertebra.

Both femora, although crushed, are complete in CMN 344 (Figure 22; Holmes et al., 2005, plate 28) and TMP 1989.097.001 (Figures 24, 34). The shafts of both femora of TMP 1989.097.001 appear thicker than in CMN 344 and other ceratopsids in general, but this may be the result of crushing. Otherwise, the femora closely resemble those described for other ceratopsids such as *Chasmosaurus* (Maidment and Barrett, 2011), *Triceratops* (Hatcher et al. 1907, fig. 71, and *Centrosaurus* (as "*Monoclonius*", Hatcher et al. 1907, fig. 86), although they (in particular those of CMN 344) appear to be somewhat more gracile. Whether this is the result of postmortem distortion, ontogeny, or represents a true morphological distinction is unclear.

Preserved epipodials in CMN 344 include the left fibula and both right and left tibiae (Figure 23; Holmes et al., 2005, plate

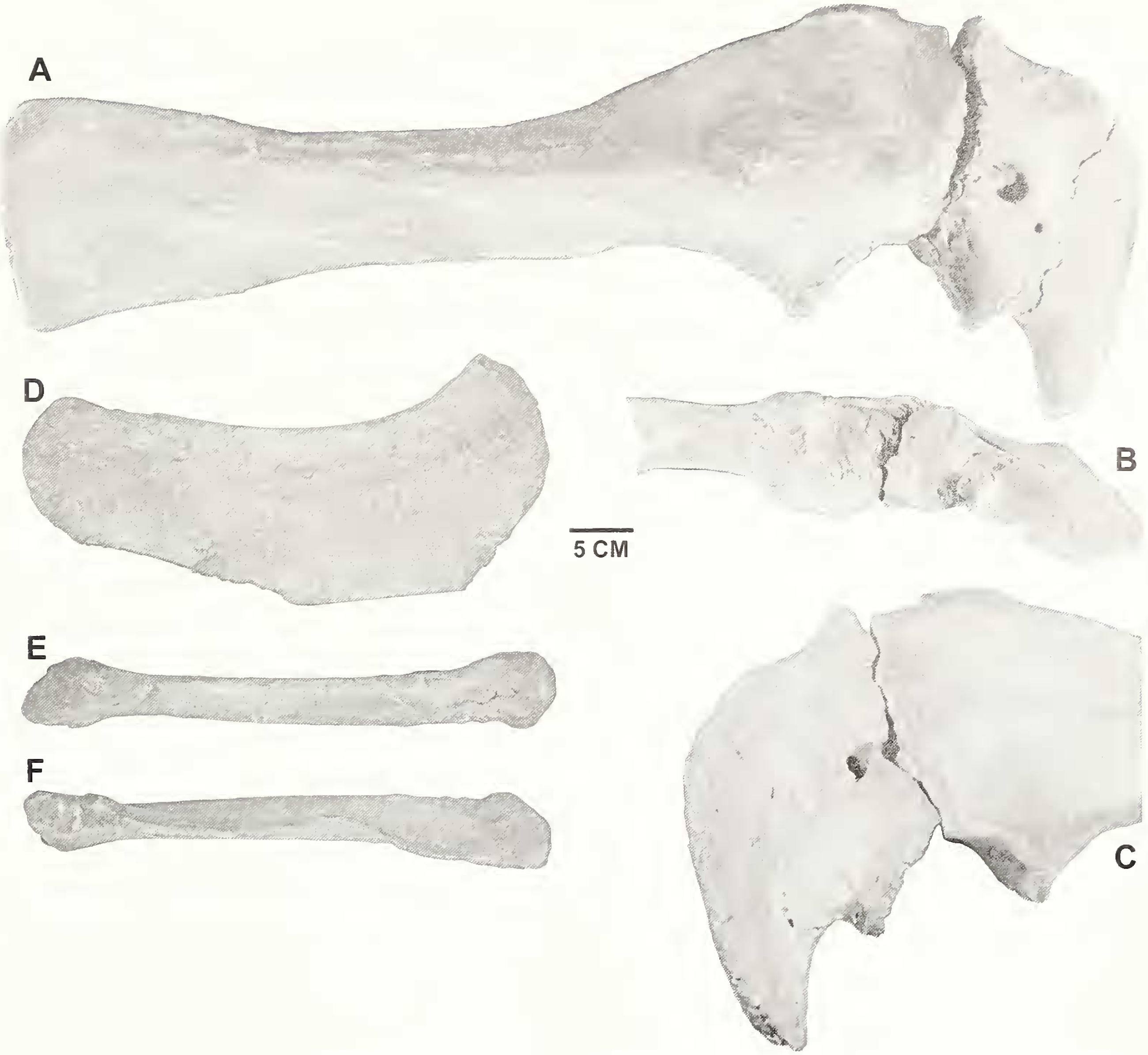

Figure 18. *Styracosaurus albertensis*, CMN 344, pectoral girdle. Right scapula with articulated coracoid in A, lateral view, B, posterior, and C, medial views. Right sternal plate in D, dorsal, E, medial, and F, lateral views. Scale bar equals 5 cm.

29), and in TMP 1989.097.001, the right tibia and fibula only. They do not differ in any obvious way from the epipodials of other ceratopsids.

The left second metatarsus is the only element of either tarsus, metatarsus and pedal elements to be preserved in CMN 344 (Holmes et al., 2005, plate 30). A virtually complete right metatarsus and pes is preserved in TMP 1989.097.001 (Figure 35). As in other ceratopsids as far as known, the medial (first) metatarsal is the shortest of the functional metatarsals (although this element seems unusually short, being less than 50% of the third metatarsal, as compared with 57% in *Centrosaurus* [Brown, 1917] and 56% in *Brachyceratops* [Gilmore, 1917]), and the third metatarsal is the longest. The second is slightly shorter than the third, as is the fourth. The latter appears to be less robust than the others, especially distally, although this could be the result of crushing. The vestigial fifth metatarsal is present, but is broken into two pieces.

As in other ceratopsids, the phalangeal formula of the pes is 2,3,4,5,0. The first (proximal) phalanx of the first digit is the longest of the proximal phalanges. In ceratopsids, as far as is known, each phalanx of second through fourth digits is shorter than its equivalent in the digit immediately medial (Dodson et al., 2004). As a result, the third digit is only slightly longer than the second digit, and the fourth digit is actually shorter than the third despite a pre-to-post axial increase in phalangeal count. This trend is more pronounced in *Styracosaurus*, in which these digits are virtually the same length (Figure 35). As a result, the digits are distinctly shorter than in *Centrosaurus*. In the latter, the length of each digit exceeds that of its corresponding metacarpal (Brown, 1917, plate xxii; Lull, 1933, fig. 29). In TMP 1989.097.001, this is

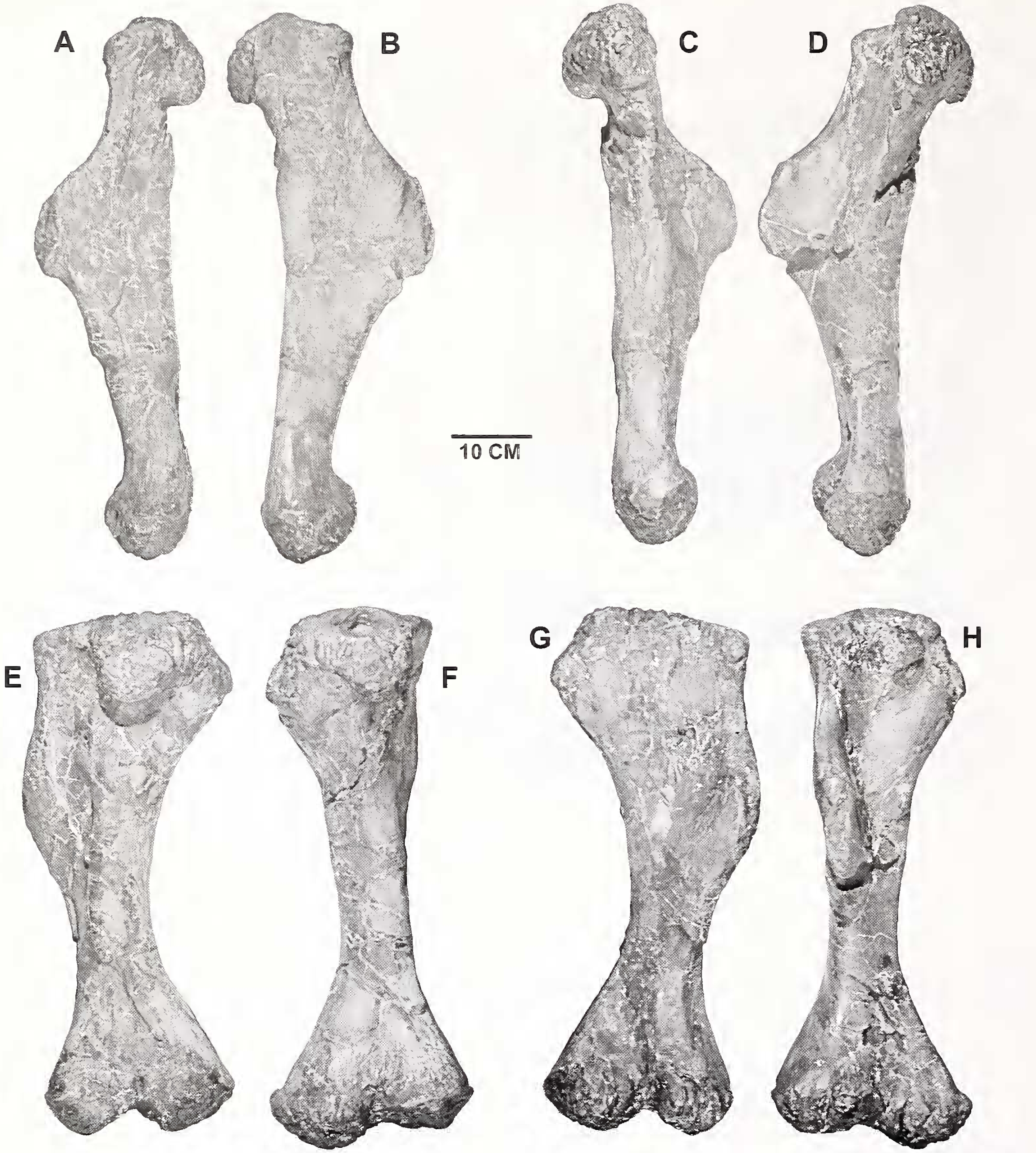

Figure 19. *Styracosaurus albertensis*, CMN 344, humeri. Left humerus in A, anterior; C, posterior; E, dorsal; and G, ventral views. Right humerus in B, anterior, D, posterior; F, dorsal, and H, ventral views. Scale bar equals 10 cm.

true of only the first and fourth digits (although even in these cases, the digits are shorter relative to their corresponding metacarpals than is the case in *Centrosaurus*). The second and third digits of TMP 1989.097.001 are actually shorter than their corresponding metacarpals. The distal ends of the terminal phalanges (unguals) of the first to third digit are highly eroded. The cause of this deformity is uncertain, but outward appearances are consistent with bone resorption. A similar morphology has been observed in *Pachyrhinosaurus* (TMP 2002.076.001, MR, pers. obs.) and large ankylosaurs (R. Sissons, pers. comm.).

Discussion

Although an enormous amount of ceratopsid material has been collected from the Upper Cretaceous deposits of North America, articulated, reasonably complete skeletons are rare. Consequently, the postcranial skeletons of most ceratopsid taxa have not been

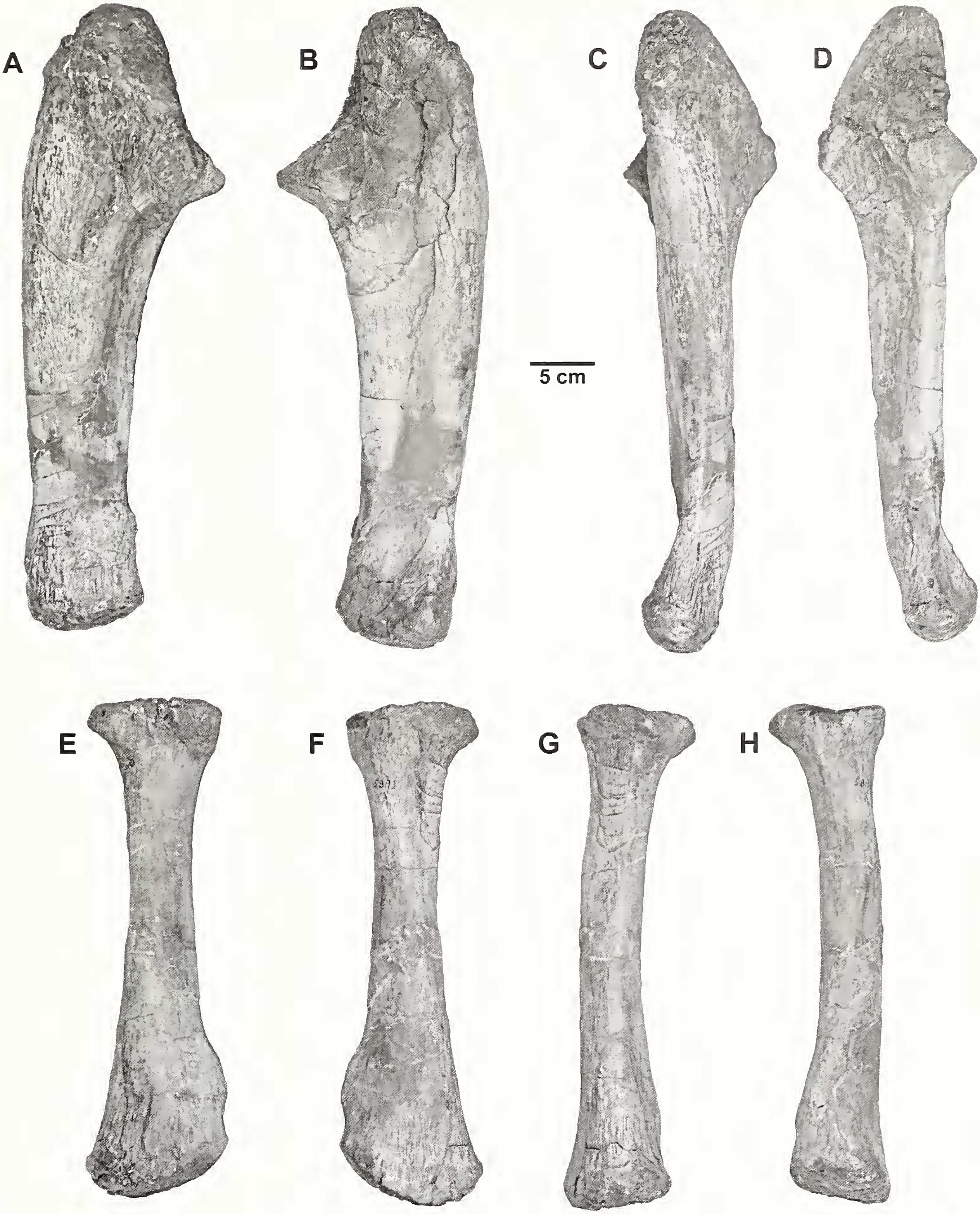

Figure 20. *Styracosaurus albertensis*, CMN 344. Right ulna in A, anterior, B, posterior, C, lateral, and D, medial views. Left radius in E, anterior, F, posterior, G, lateral, and F, medial views. Scale bar equals 5 cm.

described in sufficient detail to provide characters of phylogenetic utility (Maidment and Barrett, 2011). Notable exceptions are the centrosaurine *Centrosaurus* (Brown, 1917; Lull, 1933) and the chasmosaurine cf. *Anchiceratops* (Mallon and Holmes, 2010). In other taxa, skeletons originally described as complete or nearly so (e.g., Sternberg, 1927 for *Chasmosaurus*) have often turned out, under closer examination, to be much less complete than originally assumed (e.g., Mallon and Holmes, 2006), or, if

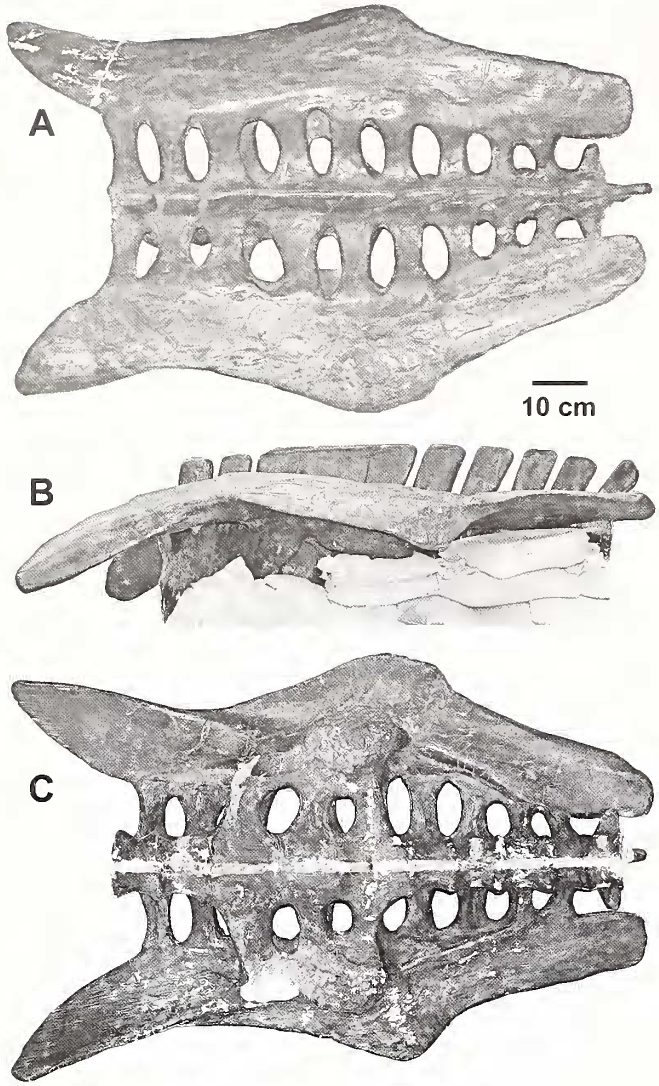

Figure 21. *Styracosaurus albertensis*, CMN 344, pelvic girdle. A, dorsal, B, left Lateral, and C, ventral views. Only the right ilium is preserved; the remainder is reconstructed in plaster. Scale bar equals 10 cm.

comprising a good percentage of the whole animal, still leave large gaps in our knowledge of the skeletal anatomy of these taxa. As a result, little is known about morphological diversity, whether rooted in intraspecific variation (including ontogenetic features and sexual dimorphism) or representing taxonomic distinctions, in the postcranial skeleton of ceratopsids. Consequently, phylogenetic analyses of the family still rest overwhelmingly on cranial characters (e.g., Dodson et al., 2004; Currie et al., 2009; Sampson et al., 2010). It is generally assumed that ceratopsids exhibit little or no inter-specific or inter-generic variability in postcranial anatomy. Although a recent morphometric study (Chinnery, 2004) generally supports this conclusion, it also indicates that some inter-subfamily differences do exist. Moreover, (Maidment and Barrett, 2011) have argued that there may be sufficient variation in discrete postcranial anatomical features to provide phylogenetically significant data. As such, a description of the postcranial skeleton of *Styracosaurus* is not only an important contribution to our understanding of ceratopsid anatomy, but also may contribute to the resolution of the phylogenetic relationships within the family. Although the results of this study do tend to support the contention that ceratopsids are quite conservative in their postcranial anatomy, comparison with the few ceratopsids for which we have significant data, in particular *Centrosaurus* and cf. *Anchiceratops* (CMN 8547), does suggest a few potentially important anatomical features that should be examined closely as more articulated skeletons are discovered.

Variation in the ceratopsid postcranial skeleton

In almost all ceratopsids, the syncervical (cervical bar) is formed by the fusion of the atlas, axis, and third cervical (Campione and Holmes, 2006; Tsuihiji and Makovicky, 2007). However, in at least one specimen (cf. *Anchiceratops*—see Mallon and Holmes, 2010), the fourth cervical vertebra fuses to the posterior end of the bar. However, it should be noted that this is essentially an extension of the process of co-ossification of the first three cervicals to form the syncervical, exhibited by all ceratopsids and at least some basal ceratopsians (Brown and Schlaikjer, 1940, 1942), and is likely an ontogenetic feature rather than one of taxonomic significance. The presence of a syncervical is almost certainly correlated with another characteristic of the family, specifically the very large head. Co-ossification of the cervical vertebrae to form a syncervical (and in the case of cf. *Anchiceratops*, the inclusion of the fourth cervical vertebra as well) presumably augmented the weight-bearing function of the cervical column.

The anterior free cervical vertebrae of both CMN 344 and TMP 1989.097.001 bear a deep pocket on the lateral surface of the centrum immediately under the base of the transverse process. The significance of this feature is uncertain. It has not been described for *Centrosaurus* (Brown, 1917; Lull, 1933), although it is present on the fourth and sixth cervicals (on the right side only) of one specimen of *Centrosaurus* (ROM 767, RH pers. obs. August, 2012). It has been described in some of the cervical vertebrae of one specimen of *Chasmosaurus* (Maidment and Barrett, 2011), but is completely absent from the well preserved cervical series in other well preserved *Chasmosaurus* specimens (CMN 2280, ROM 839, 843, RH pers. obs., August, 2012). Thus, it appears most likely that this character varies intraspecifically in ceratopsids, and is of no taxonomic significance.

Even allowing for postmortem distortion, the shapes of the vertebral centra appear to vary subtly from taxon to taxon. For example, the centra of the anterior cervicals are heart shaped in *Styracosaurus*, unlike *Triceratops*, in which they are circular to dorsally oval. This feature is hard to quantify, but vertebral centrum shape may still prove to be a valid feature to distinguish the vertebrae of various ceratopsid taxa.

Styracosaurus and *Centrosaurus* both show a progressive decrease in centrum length throughout the cervical series. In at least one specimen of *Chasmosaurus* (NHMUK R4948), both dimensions remain sub-equal throughout the cervical series (Maidment and Barrett, 2011, fig. 17), suggesting the possibility that this might represent a distinction between the two subfamilies. However, in another specimen of *Chasmosaurus* (CMN 2280), there is a subtle, but clear anteroposterior reduction in centrum length in the cervical column. This also appears to be the case in at least one specimen of *Triceratops* (Ostrom and Wellnhofer, 1986, plates 2–4). This may simply be an intraspecifically variable character and of no taxonomic significance in ceratopsids, but more complete, well preserved cervical columns are required to resolve this.

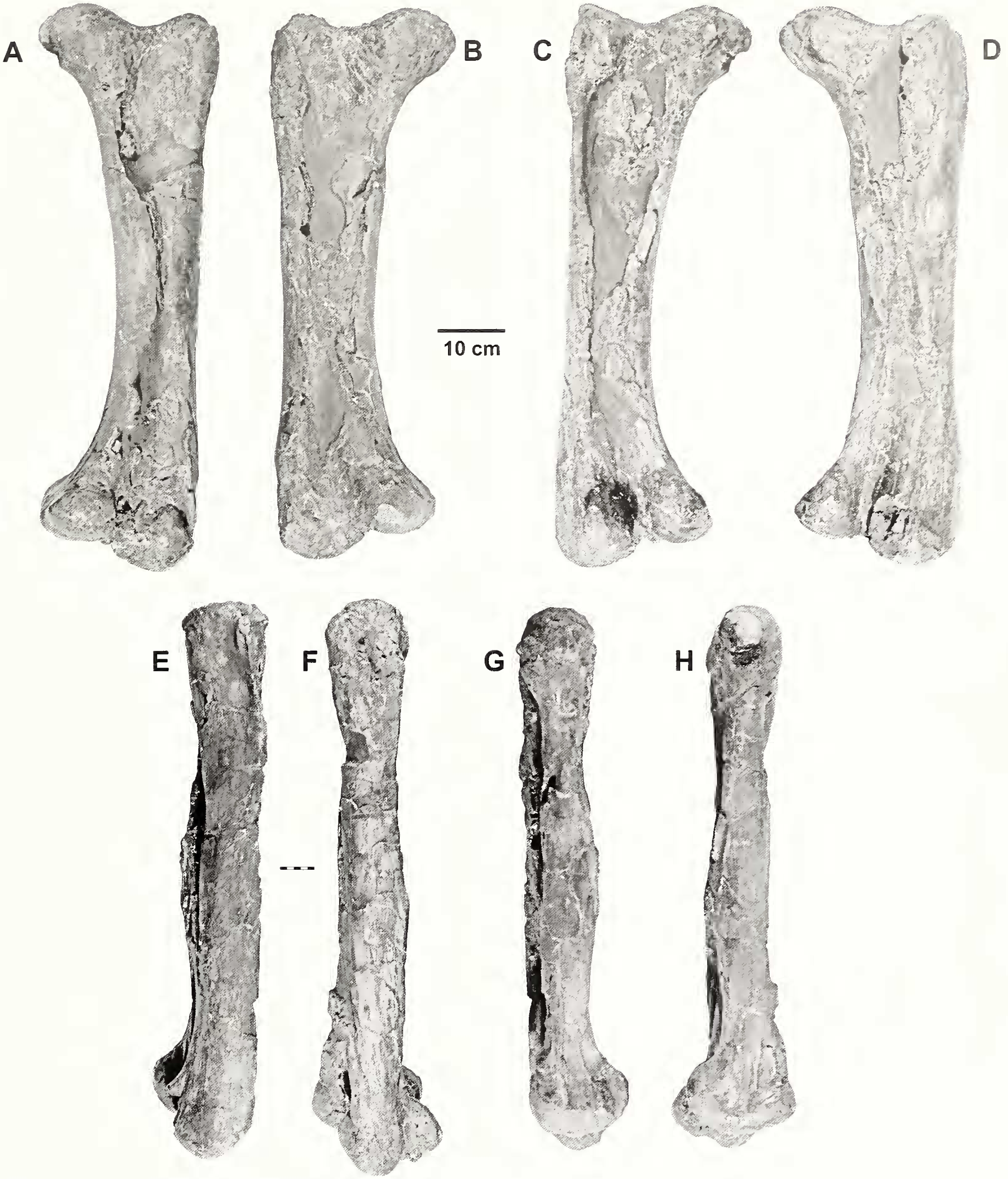

Figure 22. *Styracosaurus albertensis*, CMN 344, femora. Left femur in A, Anterior, C, posterior, E, lateral, and G, medial views. Left femur in B, anterior, D, posterior, F, lateral, and H, medial views. Scale bar equals 10 cm.

The number of cervical vertebrae is also known to vary within ceratopsids, although much of the apparent variability recorded in the literature can be traced to differing interpretations of syncervical structure and definitions of what constitutes a cervical vertebra. The syncervical has been hypothesized to have been derived by the fusion of either three or four vertebrae (see, e.g., Hatcher et al., 1907; Brown, 1917; Ostrom and Wellnhofer, 1986; Dodson et al., 2004). However, it now appears almost certain that

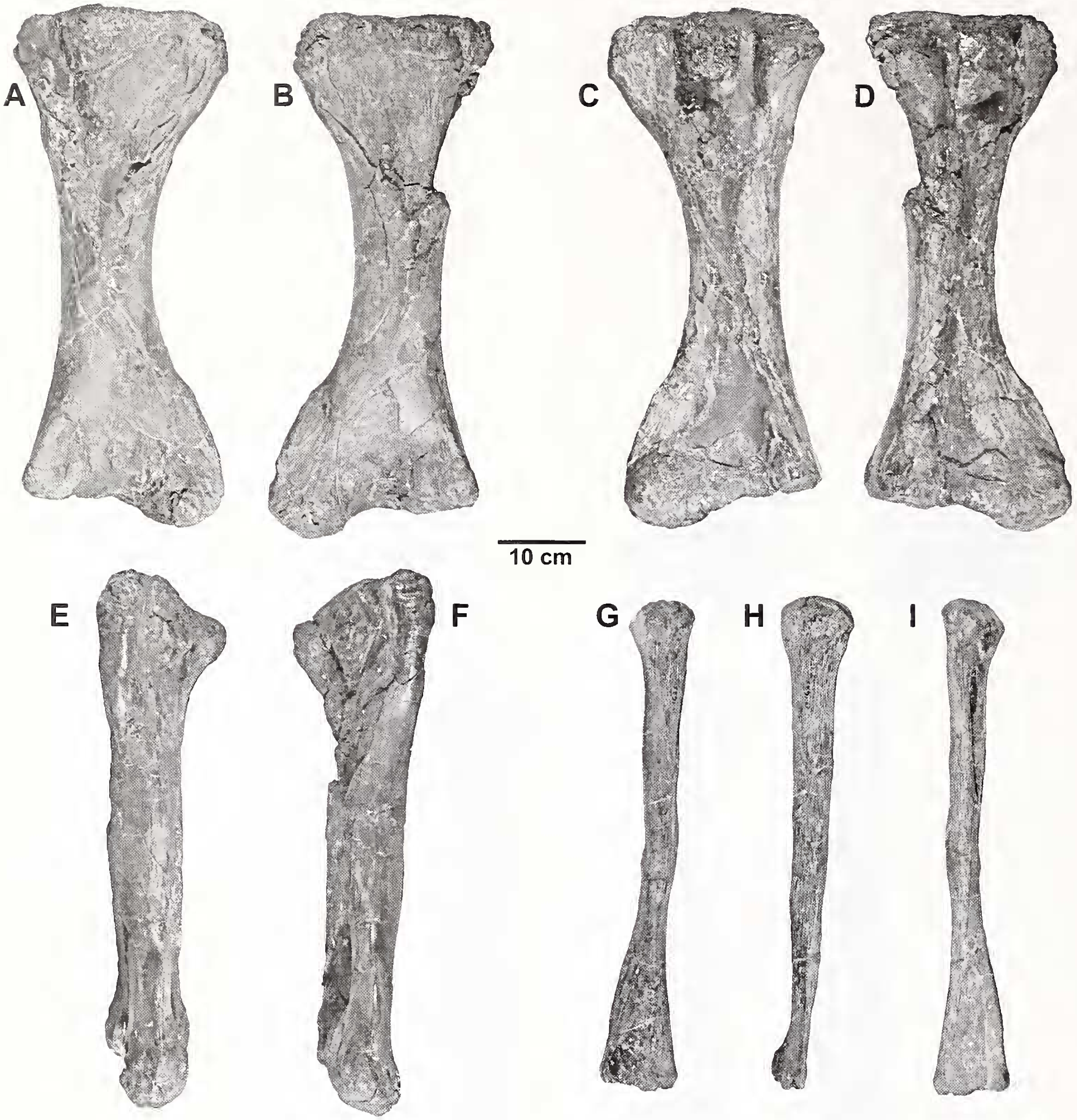

Figure 23. *Styracosaurus albertensis*, CMN 344. Left tibia in A, anterior; C, posterior, and E, lateral views. Right tibia in B, anterior, D, posterior, and F, lateral views. Left fibula in G, anterior, H, posterior, and I, medial views. Scale bar equals 10 cm.

it comprised only three vertebrae (Campione and Holmes, 2006; Tsuihiji and Makovicky, 2007), effectively reducing the cervical count by one vertebra. Identification of the transition point between the cervical and dorsal columns has also proved to be contentious. Most authors define a ceratopsid cervical vertebra as possessing the lower rib facet (parapophysis) on the lateral surface of its centrum (e.g., Brown, 1917). They identify the transition to the first dorsal vertebra at the point where there is an abrupt shift of the parapophysis from the side of the centrum to the underside of the transverse process. A more subjective definition of this transition is associated with a gradual increase in the size and orientation of the neural spine and transverse processes (e.g., Hatcher et al., 1907; Ostrom and Wellnhofer, 1986) as well as enlargement of the neural canal and larger and more ventrally directed ribs associated with the transitional vertebrae (Lull, 1933). The unstated assumption appears to be that the enlarged neural canal for accommodation of the brachial plexus, as well as the presence of ribs long enough to have articulated with the sternum (and therefore contributed to the formation of the rib cage) indicate that these vertebrae should be considered to be part of the thoracic column. However, it has been demonstrated (Giffen, 1995) that in a wide variety of tetrapods, the brachial

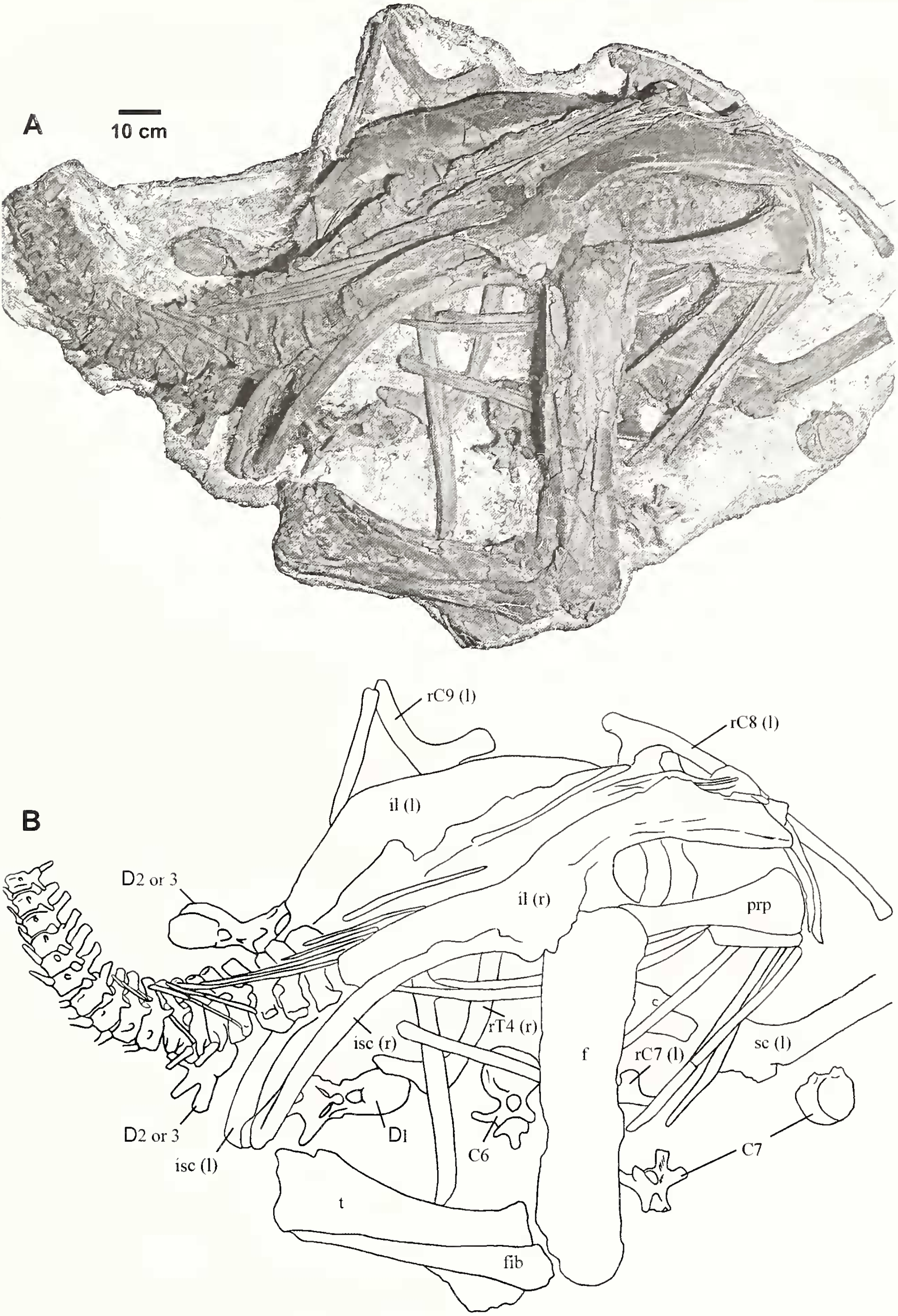

Figure 24. *Styracosaurus albertensis*, TMP 1989.097.001, pelvis, right rear limb, proximal caudal region, disarticulated vertebrae and ribs. A, photograph of specimen. B, outline drawing of specimen. Scale bar equals 10 cm.

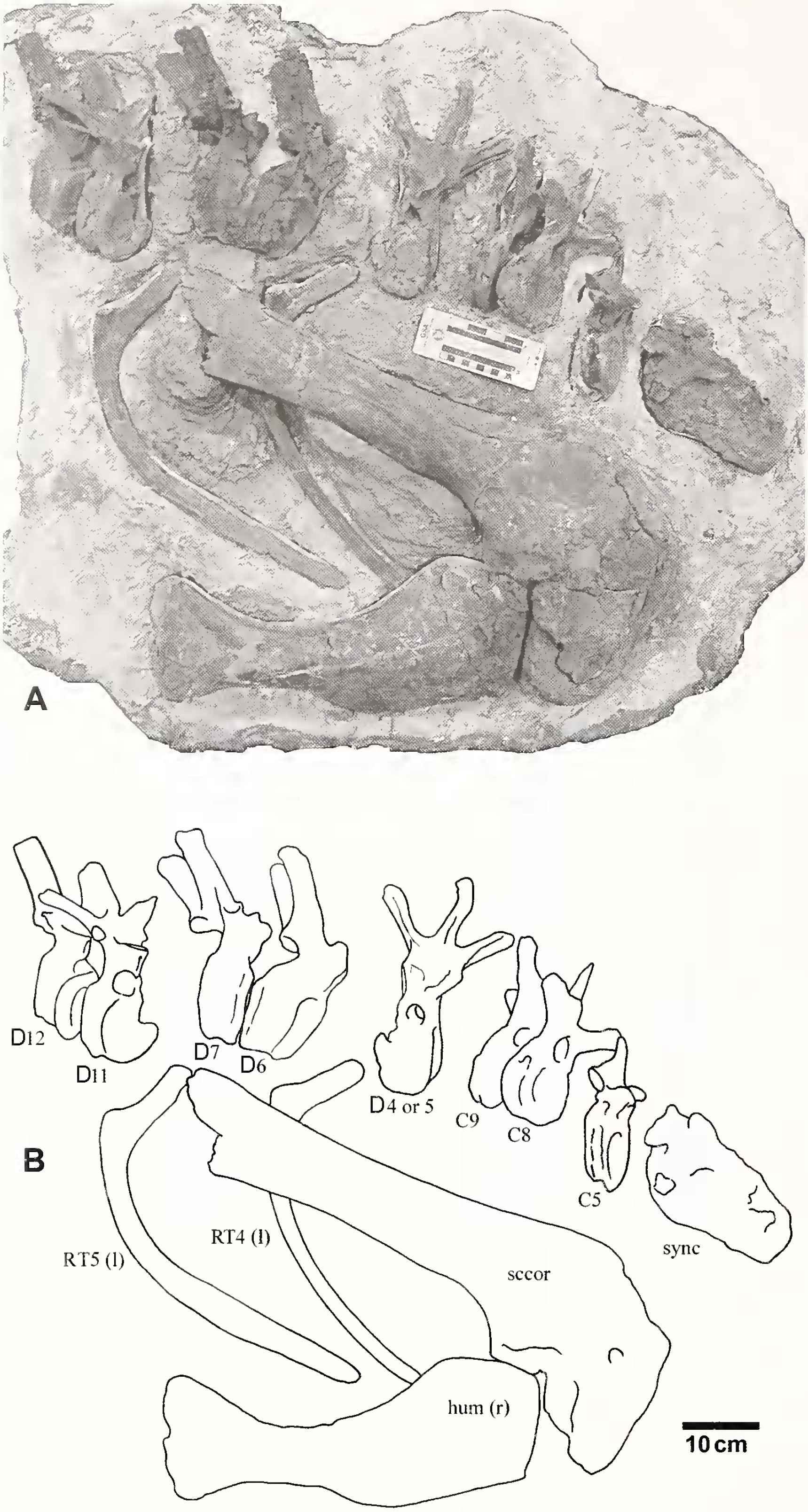

Figure 25. *Styracosaurus albertensis*, TMP 1989.097.001, partial vertebral column, right pectoral girdle, and limb. A, photograph of specimen as mounted. B, outline drawing of specimen. Scale bar equals 10 cm.

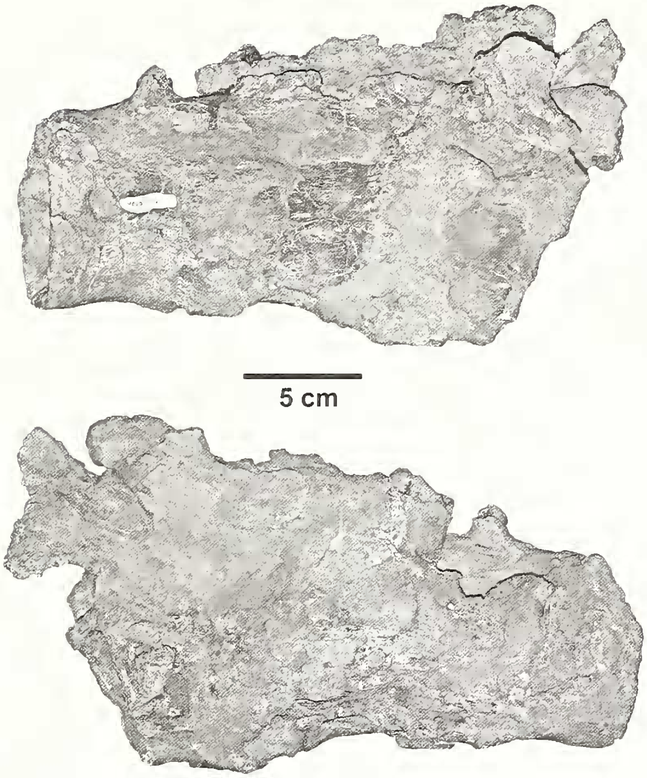

Figure 26. *Styracosaurus albertensis*, TMP 1989.097.001, syncervical. A, left lateral, and B, right lateral views.

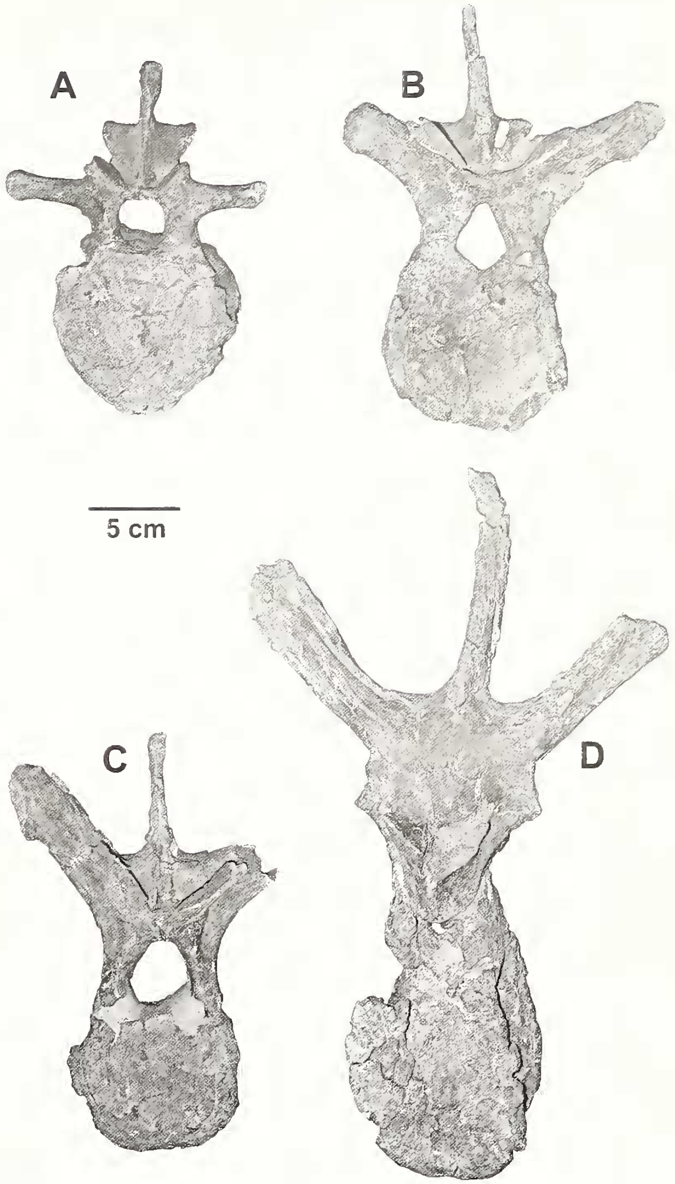

Figure 27. *Styracosaurus albertensis* TMP 1989.097.001. Vertebrae in anterior views. A, C5. B, C8. C, C9. D, D4 or 5. Scale bar equals 5 cm.

plexus is primarily associated with the posterior cervicals, with only relatively minor contributions from the most anterior few dorsal segments. Nevertheless, the ribs of the ninth vertebra (last cervical sensu Brown 1917, or second dorsal sensu Lull, 1933; Ostrom and Wellnhofer, 1986) appear to have had cartilaginous connections to the sternum, suggesting that it might be more properly considered, at least functionally, as part of the dorsal series. However, it must be remembered that the shoulder girdle of ceratopsid dinosaurs was located quite far forward on the body, and almost certainly encroached on the neck region (Figure 1). We suggest that the forward migration of the pectoral girdle is a specialization of the larger, quadrupedal ceratopsids. Why this should have occurred is uncertain, but it may have evolved to help support the large (and heavy) head characteristic of these animals. During the process, it 'captured' two ribs (and their associated vertebrae) whose homologies lie with the posterior cervical region. Although these ribs are modified to serve as part of the thoracic cage (being elongate, although only the more posterior has established a connection with the sternum for support), they both retain the diagnostic cervical rib articulation.

If it is accepted that the syncervical is tripartite, and that the transition from the cervical to thoracic region is marked by an abrupt transition of the parapophysis from the lateral surface of the centrum to the underside of the transverse process, then most ceratopsids have nine cervical and 12 dorsal vertebrae. This is true of *Centrosaurus* (Brown, 1917; Lull, 1933) and *Chasmosaurus* (CMN 2245, 2280, Mallon and Holmes, 2006; ROM 843, RH pers. obs., August, 2012, contra Maidment and Barrett, 2011).

The type specimen of *Styracosaurus* exhibits these cervical and dorsal counts, but because the sacrum is not preserved, the number of dorsosacrals is unknown. TMP 1989.097.001 is incomplete, comprising one less cervical and four fewer dorsal vertebrae, but each of the preserved presacral vertebrae can be confidently matched to its homologue in the type (CMN 344). The absence of any vertebrae showing morphology distinct from any of the type vertebrae suggests that it is unlikely that any of the vertebrae of the latter are missing, and a total of 21 presacrals is the true count for *Styracosaurus*. However, some variation in vertebral numbers is known to exist within ceratopsids. At least one specimen of cf. *Anchiceratops* (CMN 8547) has 10 cervicals rather than nine, and the thorax comprises 13 (rather than 12) vertebrae, for a total of 23 presacral vertebrae (Mallon and Holmes, 2010).

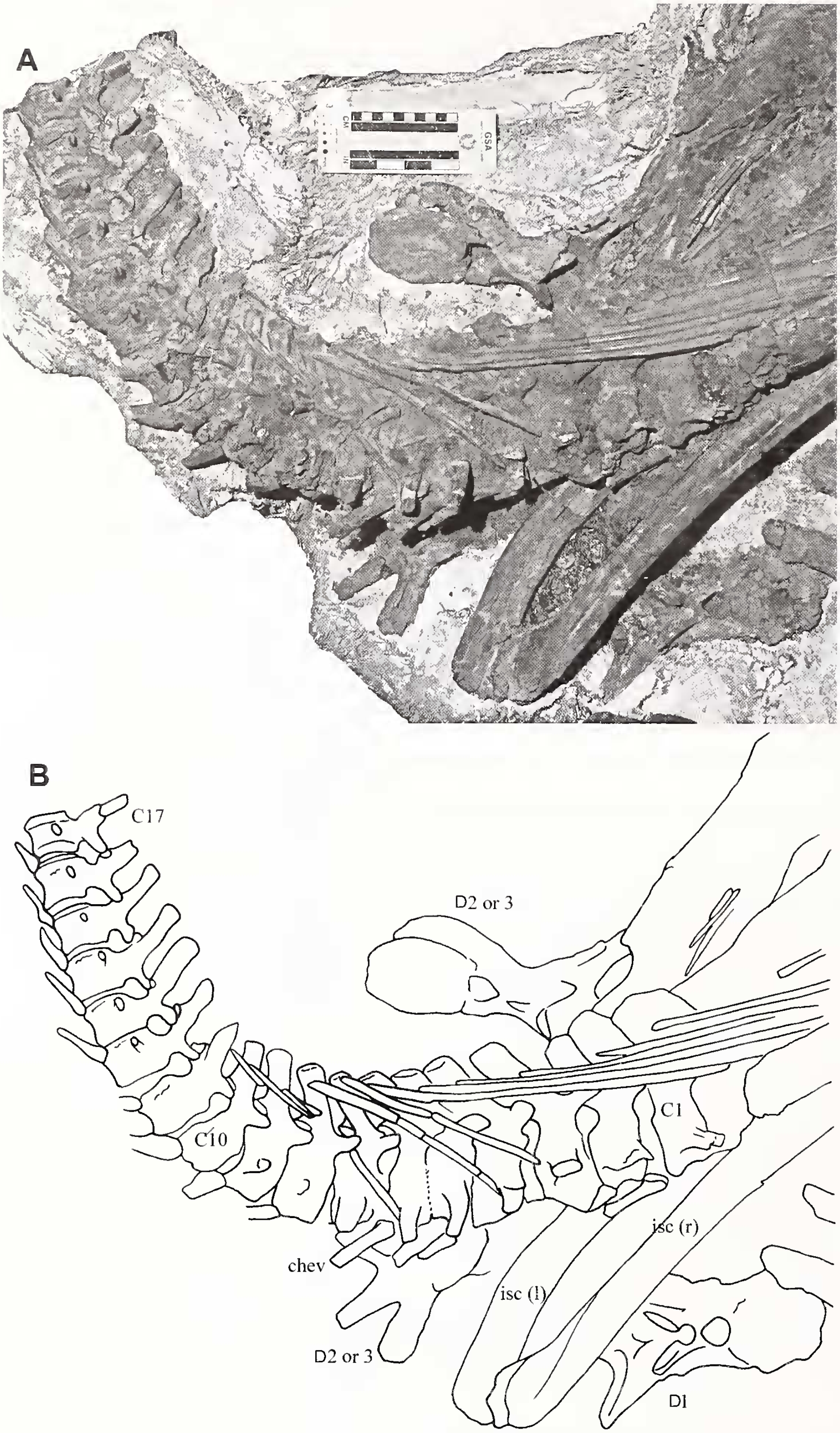

Figure 28. *Styracosaurus albertensis* TMP 1989.097.001. Articulated proximal portion of the tail. A, photograph of the specimen. B, outline drawing of the specimen.

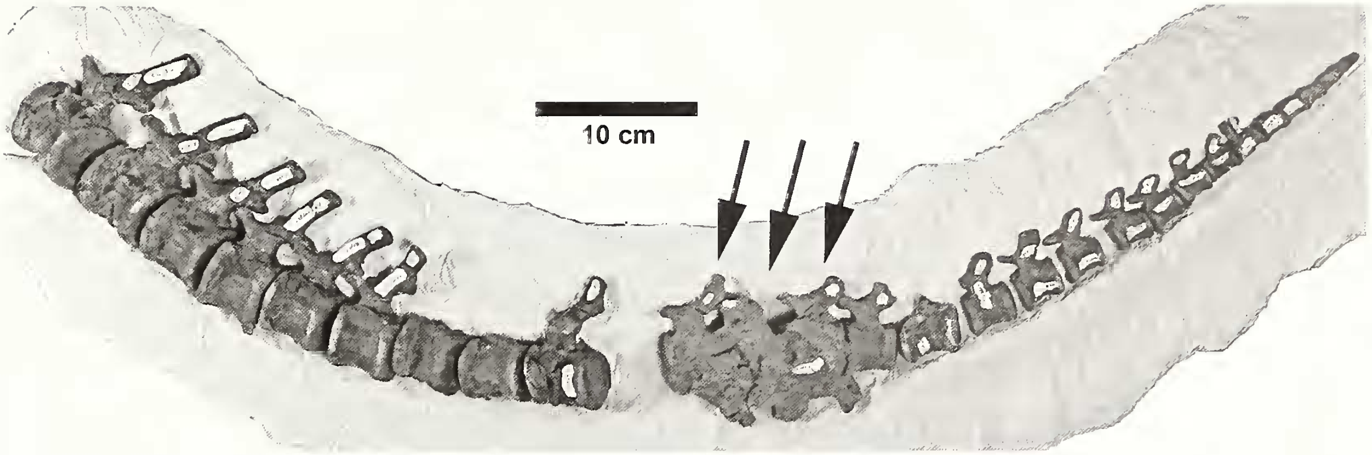

Figure 29. *Styracosaurus albertensis*, TMP 1989.097.001, caudal vertebrae 18–45 in left lateral view. Arrows indicate region of pathological vertebrae. Scale bar equals 10 cm.

The sacrum of ceratopsids comprises four co-ossified vertebrae. A variable number of vertebrae, usually referred to as dorsosacrals, co-ossified to the front of the sacrum. Together with the sacrum and a variable number of caudal vertebrae that fused to the posterior end of the sacrum, they comprise the sacral bar. Most commonly, ceratopsids have one dorsosacral between the 12th dorsal vertebra and the first sacral vertebra. This condition has been reported in *Centrosaurus* (Brown, 1917: plate XIIB; Lull, 1933, fig. 18). The same count occurs in some specimens of *Chasmosaurus* (CMN 2245 contra Maidment and Barrett, 2011). This is precisely the same count seen in the basal ceratopsians *Protoceratops* (Brown and Schlaikjer, 1940), *Montanoceratops* (Brown and Schlaikjer, 1942), and possibly *Leptoceratops* (CMN 8889, RH, pers. obs., August, 2012), suggesting that this is most likely the primitive count for ceratopsids. However, it should be noted that although *Leptoceratops* (CMN 8889) possesses a single dorsosacral bearing a roughened posterior centrum articulation that suggests incomplete co-ossification with the element posterior to it, the sacrum is not preserved. Therefore, it is uncertain whether it articulated with the first sacral vertebra, or a second (unpreserved) dorsosacral. The type of *Styracosaurus* shares these cervical and dorsal counts, but the sacrum is not preserved, and the number of dorsosacrals is unknown.

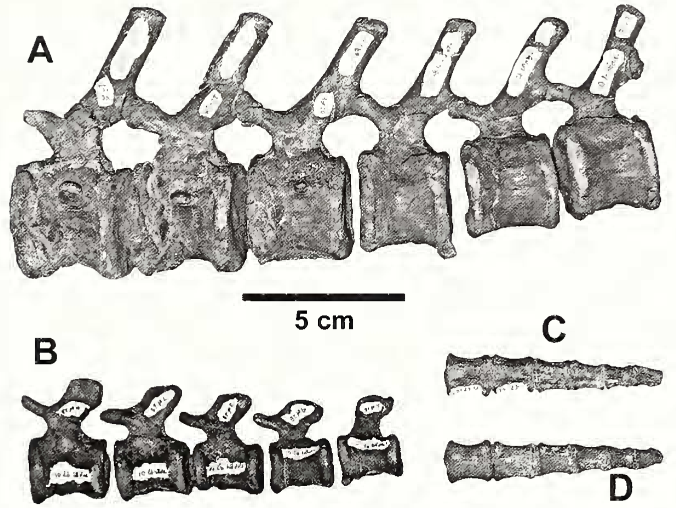

Figure 30. *Styracosaurus albertensis*, TMP 1989.097.001, caudal vertebrae. A, Ca18–23 in left lateral view. B, Ca33–37 in left lateral view. Terminal six (Ca40–45) in C, dorsal and D, ventral views. Scale bar equals 5 cm.

Dorsosacrals are most parsimoniously homologized with posterior dorsal vertebrae that were incorporated at some point in the ontogeny of the individual into the sacral bar. In at least one specimen of *Centrosaurus* (Lull, 1933), the last (12th) dorsal vertebra had begun to fuse to the front of the synsacrum at the time of death, effectively becoming a second dorsosacral. Essentially the same condition has been described in *Pentaceratops* (Wiman, 1930; Lehman, 1998, fig. 6). However, the number of dorsosacrals appears to vary from individual to individual (or possibly taxon to taxon). This could plausibly be accounted for by progressive incorporation of posterior dorsal vertebrae into the sacral bar during growth, except that the increase in the number of dorsosacrals is not always compensated for by a corresponding reduction in the number of dorsal vertebrae. *Vagaceratops* (=*Chasmosaurus*) *irvinensis* (CMN 41357) has two dorsosacrals fused to the front of the sacral bar (RH, pers. obs., February,

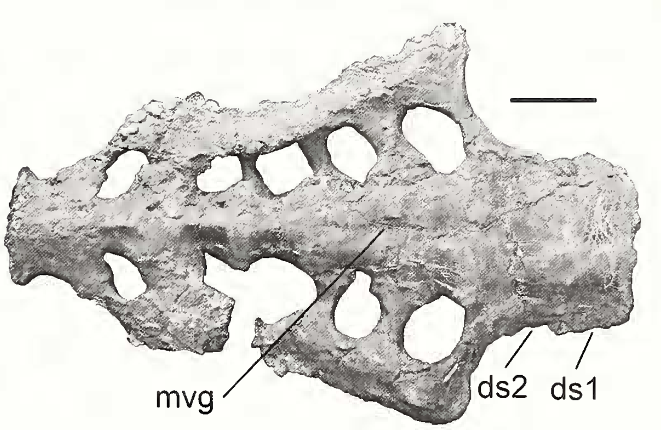

Figure 31. *Styracosaurus albertensis*. TMP 2009.080.001. Ventral view of synsacrum. Scale bar equals 10 cm.

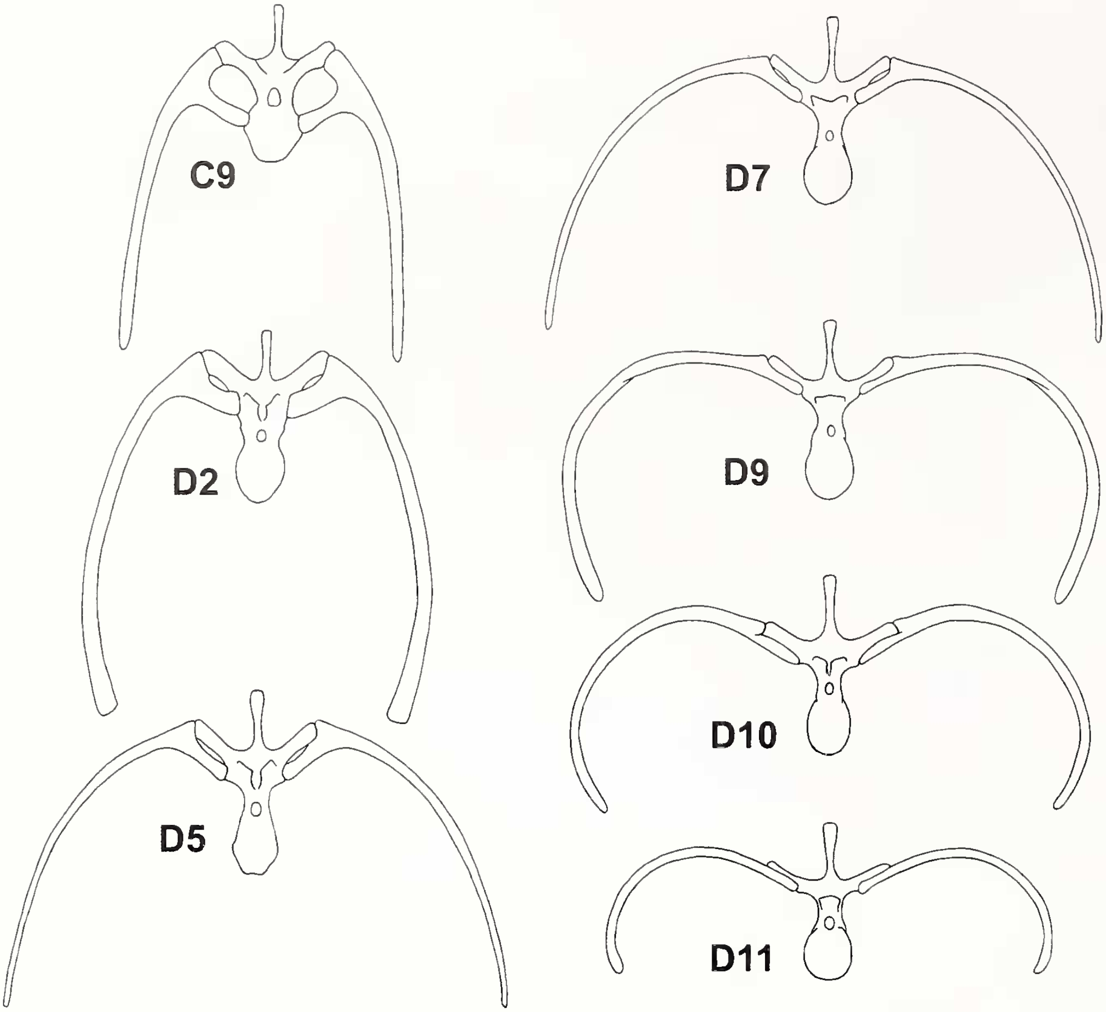

Figure 32. *Styracosaurus albertensis*. Vertebrae and associated ribs from selected points in the presacral column in anterior view.

2012). The more anterior vertebra (13th postcervical) bears a pair of flat, laterally and slightly anteriorly projecting ribs fused to the ends of the diapophyses. Very similar (although unfused) ribs have been described in association with the 12th postcervical rib in *Centrosaurus* (Lull, 1933). In the latter taxon, they lie along the inner surface of the ilium (the ilium is not preserved in CMN 41357). In one specimen of *Chasmosaurus* (ROM 843), there are two dorsosacrals between the last (12th) dorsal and first sacral vertebrae. The first bears a pair of flat, anterolaterally directed ribs that articulate throughout most of their lengths with the dorsomedial edge of the ilium. The rib, which bears no capitulum, is fused to the end of the transverse process, but the suture is still visible. The more posterior dorsosacral bears dorsoventrally flattened, distally expanded transverse processes that articulate with the ilium. No separate rib is evident. This specimen is unusual in that the last dorsal (12th) vertebra fused to the anterior end of the sacral bar before death (so is functionally a dorsosacral), leaving only 11 free dorsal vertebrae. However, a cast of the specimen, on display at the Royal Ontario Museum has a dorsal series comprising 12 free vertebrae in addition to the three vertebrae fused to the anterior end of the sacrum. Close examination of the cast revealed that two of the vertebrae (probably representing D8 or D9) in the mount are exact duplicates (RH, pers. obs., August, 2012)—apparently an extra vertebra was cast during the preparation of the mount and added to the vertebral column, presumably because the technicians believed that one had been lost. This appears to be the source of the unusually high presacral + dorsosacral count reported for this specimen (Maidment and Barrett, 2011).

Triceratops is problematic (Ostrom and Wellnhofer, 1986). Hatcher (1907) appears to suggest that there are two dorsosacrals in USNM 4842 (Hatcher, 1907, figs. 53, 54), but equivocates. However, in the recently described *Triceratops* specimen (NSM PV 20379), 21 presacral vertebrae are identified (Fujiwara, 2009, fig. 2), but the rib associated with the last (his 'p21') looks more like the rib associated with the 11th dorsal vertebra of other ceratopsids (note its anterior curvature and articulation with the pubis) and the rib associated with 's1' (the 22nd presacral) is directed strongly anteriorly and appears to lie along the medial surface of the ilium, much like that of the 21st presacral rib of *Styracosaurus*, suggesting that NSM PV 20379 has one vertebra more than the usual 22 presacrals + one dorsosacral.

A major difficulty in assessing the significance of dorsosacral count is that in many ceratopsid specimens the sacrum is not preserved, or is obscured by the ilium so that the precise location of the first sacral vertebra cannot be established. Without being

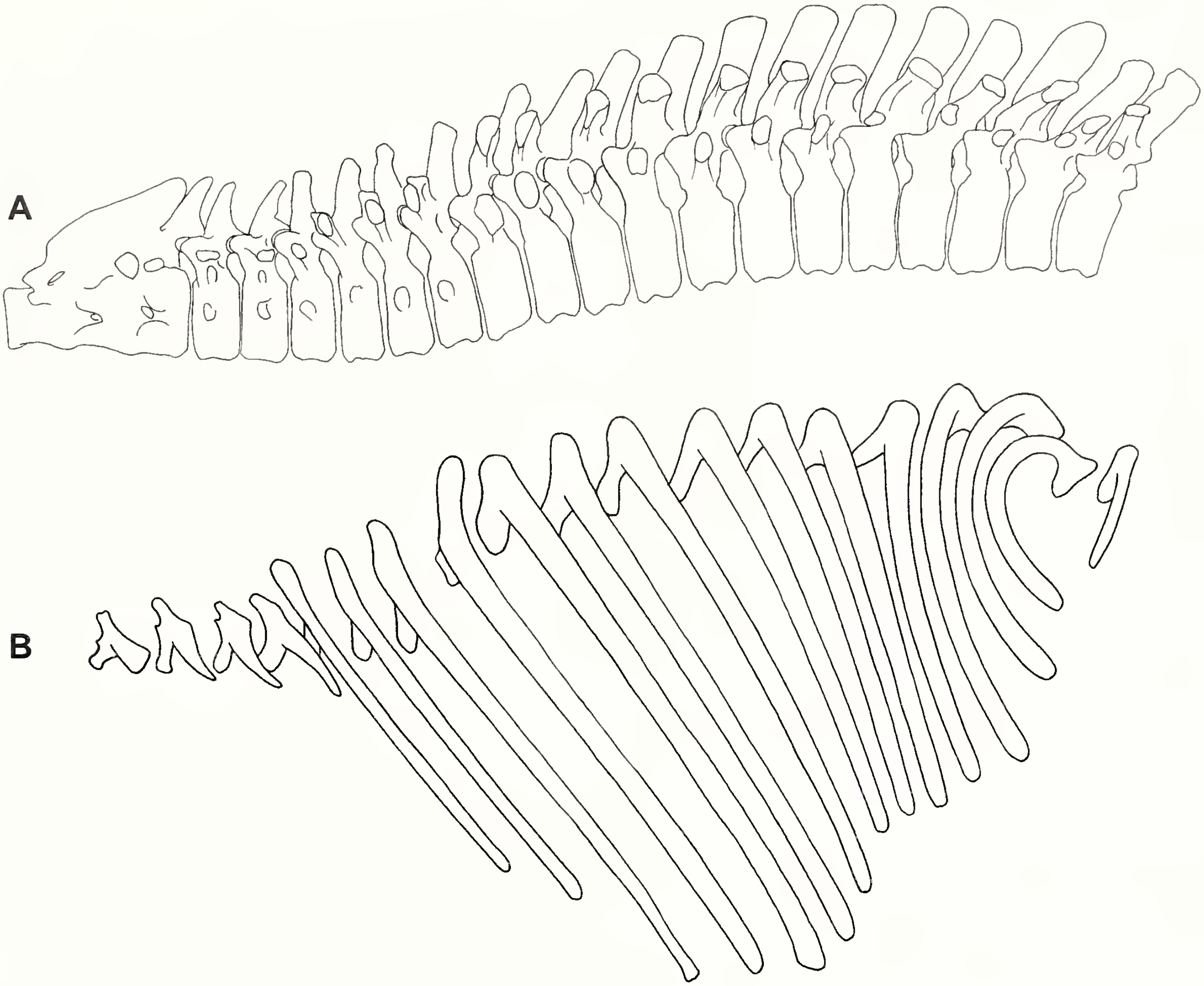

Figure 33. *Styracosaurus albertensis.* A, presacral column in left lateral view, B, set of ribs (C3 to D12) in left lateral view drawn to the same scale as vertebrae in A.

able to establish the position of the sacral vertebrae, it is not possible to distinguish dorsosacrals from late fusing posterior dorsal vertebrae. Such is the case in *Styracosaurus*. The sacrum is not preserved in the type (CMN 344). Although the pelvis and sacrum of TMP 1989.097.001 appear to be complete, the sacral ribs are obscured by the ilia. The only known sacrum that can be unambiguously identified as pertaining to *Styracosaurus* (TMP 2009.080.001, Figure 31) includes two putative dorsosacrals, but as most of the disarticulated presacral column is not preserved in this specimen, it is impossible to determine whether this is in addition to the regular 21 presacrals (i.e., homologous to the dorsosacral of most other ceratopsids), or represents a fusion of the last (presumably 21st) dorsal vertebra to the sacral bar, as occurs in one specimen of *Centrosaurus* (Lull, 1933).

Although it is reasonable to assume that the number of proximal caudal vertebrae that become incorporated into the sacral bar as caudosacrals also varies with age and/or taxon, data are even scarcer than they are for dorsosacrals. In one specimen of *Centrosaurus* (Lull, 1933), there are five caudosacrals fused to the sacrum, but the transverse processes of the most posterior vertebra do not contact the ilium. *Pentaceratops* is described as having four caudosacrals (Wiman, 1930, plate V), as is *Triceratops* (USNM 4842—see Hatcher et al., 1907, fig. 53, 55) although, as described for *Pentaceratops*, the transverse processes of the most posterior vertebra are short and do not contact the ilium. *Chasmosaurus* (ROM 843) has four caudosacrals (Maidment and Barrett, 2011), but again, the anterolaterally-directed transverse processes more closely resemble those of the proximal caudal vertebrae, and do not articulate with the ilium.

Very few ceratopsids have complete tails. Available data suggest that chasmosaurines had shorter tails than centrosaurines, although the possibility of intra-generic, or even intra-specific variation within ceratopsians (e.g., Hone, 2012) renders this generalization potentially problematic. Nevertheless, it is known that *Pentaceratops* has perhaps a few more than 30 caudal vertebrae (Wiman, 1930). The most complete *Chasmosaurus* tail (CMN 2245) has only 21 vertebrae (see Mallon and Holmes, 2006, fig. 3; pers. obs., March, 2011), but judging from the size of the most distal element, the complete tail could not have comprised more than 40 vertebrae. At least one specimen of cf. *Anchiceratops*

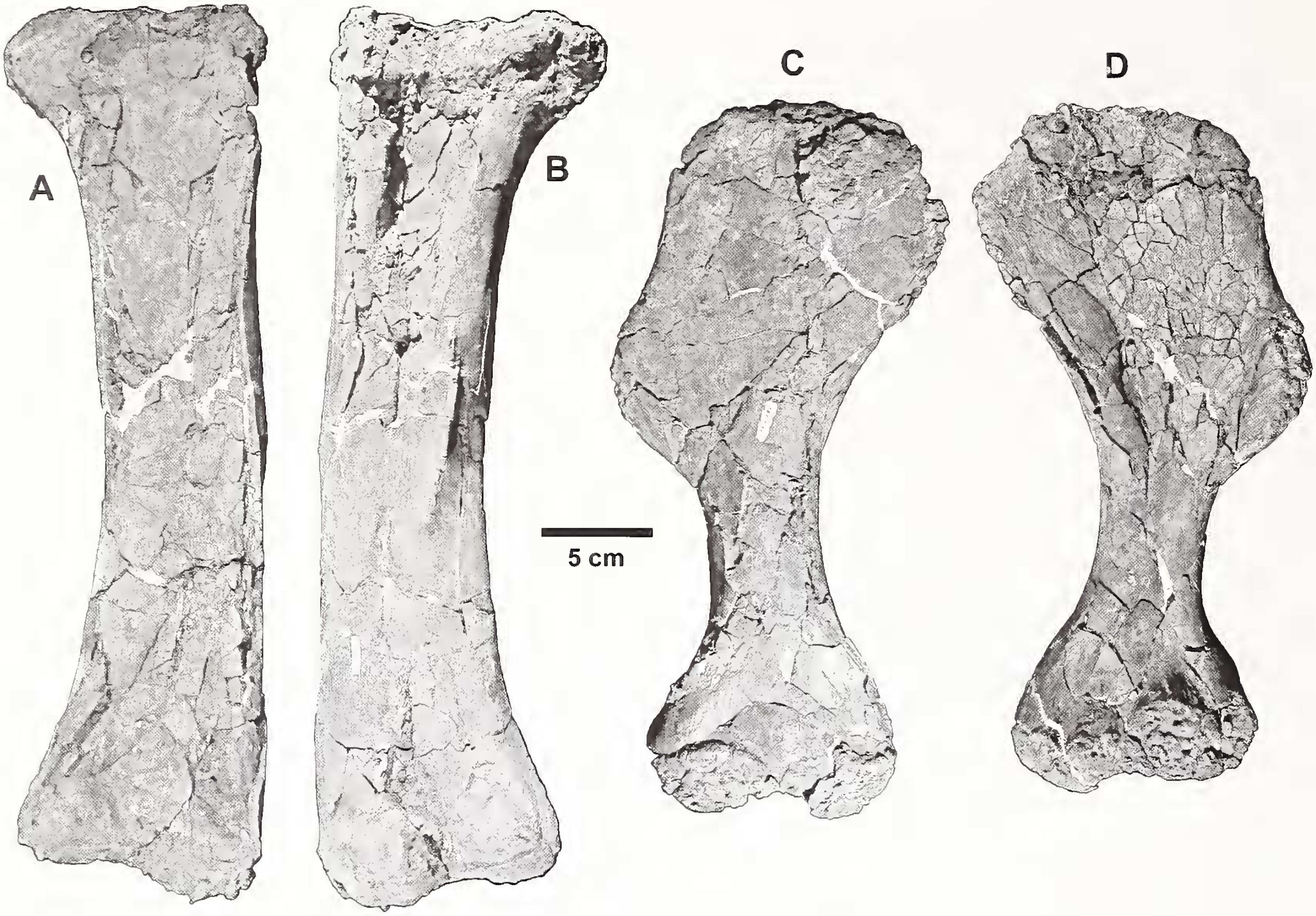

Figure 34. *Styracosaurus albertensis*, TMP 1989.097.001. Left femur in A, dorsal and B, ventral views. Humerus in C, dorsal and D, ventral views. Scale bar equals 5 cm.

(CMN 8547) has 39 caudal vertebrae (Mallon and Holmes, 2010), but this may be related to the combination of a posterior migration of the pelvis, in effect 'creating' one extra cervical and one extra dorsal vertebra, and the incorporation of two extra vertebrae into the synsacrum (see above), essentially removing two more segments from the tail of this individual. Even so, the caudal count would be very close to that reconstructed for *Chasmosaurus*. Centrosaurines, as far as is known, have higher counts, with 46 in *Centrosaurus* (Brown, 1917), 45 in *Styracosaurus*, and 47 in *Brachyceratops* (Gilmore, 1917).

The first four cervical ribs of *Styracosaurus* (C3 to C6) are quite short. The fifth (C7) is considerably longer, being at least two-thirds the length of the longest thoracic rib. The ribs at C8 and C9 become gradually longer. This resembles the situation in *Centrosaurus* (Brown, 1917), but is distinct from that in *Triceratops*, where the ribs on C7 are also short (Hatcher et al., 1907; Ostrom and Wellnhofer, 1986), and so there is an abrupt increase in rib length at the eighth cervical vertebra. In cf. *Anchiceratops*, the seventh cervical rib shows the same morphology as the more anterior ribs in having a short, upturned, spine-like shaft. The eighth rib has a more conventional posteroventrally directed shaft, but it is still quite short. The ninth cervical rib is much longer (its shaft is about 2/3 the length of the longest trunk ribs) and stouter, and the tenth (last) cervical rib is as long as the longest trunk ribs. These differences between the ribs of cf. *Anchiceratops* and those of other ceratopsids is presumably correlated to the possession of an extra cervical vertebra in this taxon.

Maidment and Barrett (2011) have suggested that the morphology of the acromial process of the scapula differs in the two subfamilies, with the process being larger and more conspicuous in chasmosaurines. In *Styracosaurus*, the process is actually quite prominent, curving laterally from its base, albeit restricted to the proximal end of the scapula, as pointed out by Maidment and Barrett (2011). Essentially the same morphology is seen in *Centrosaurus* (AMNH 5351, RH pers. obs., August, 2012). In at least some specimens of *Chasmosaurus* (CMN 2245, NHMUK R4948), the process is very indistinct, and appears to be represented by a low, but much longer crest that sweeps farther distally on the anterior edge of the scapula. However, in the chasmosaurine *Triceratops*, the process is quite distinct (Hatcher et al., 1907, fig.64), suggesting that relative size and shape of the process may be an ontogenetic or allometric feature.

The form of the humerus may differ between the two subfamilies as well (Chinnery, 2004; Maidment and Barrett, 2011). Two features mentioned by the latter authors, the relative size of the triceps fossa and the size and position of the foramen that possibly marks the insertion of the latissimus dorsi, were

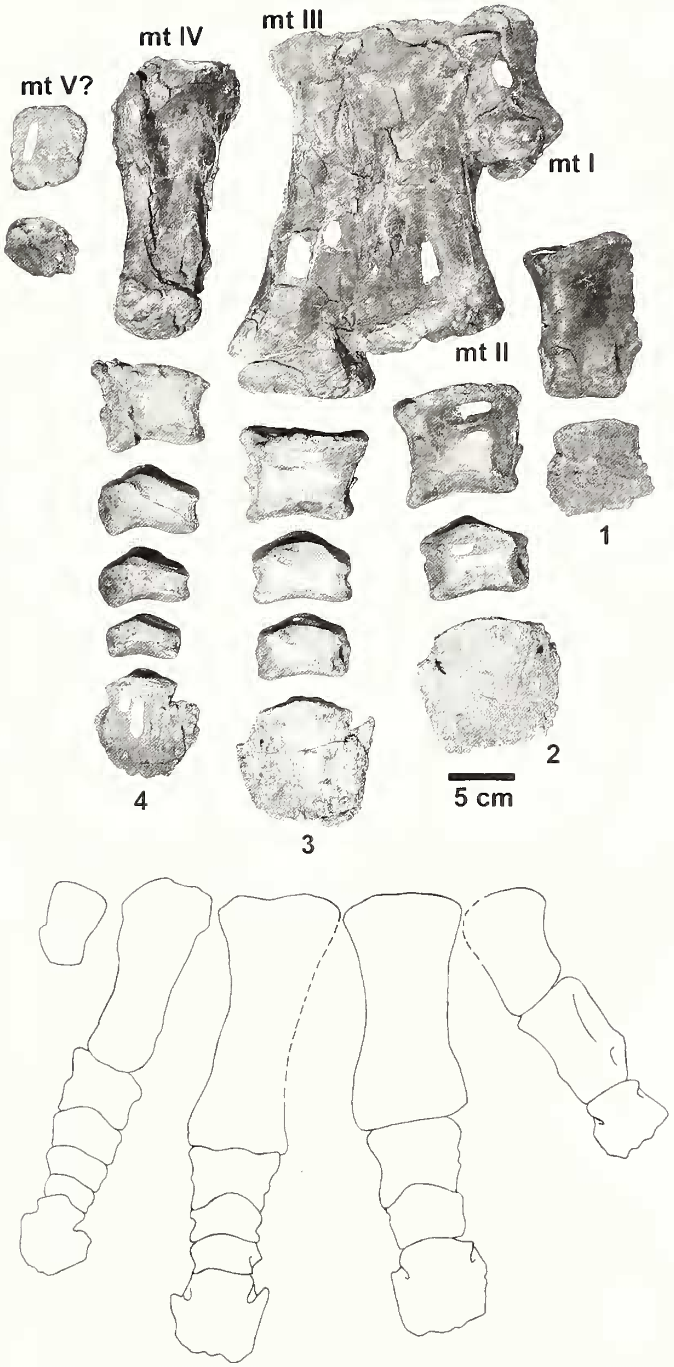

Figure 35. *Styracosaurus albertensis*, TMP 1989.097.001, right pes in dorsal view. Exploded (upper) and articulated (lower). Scale bar equals 5 cm.

difficult for us to assess in most of the specimens we examined as a result of crushing and/or poor preservation. However, the morphology of the proximal humeral head is more often preserved, and we confirm Maidment and Barrett's (2011) observation that the anterior margin of the deltopectoral crest is arched distinctly dorsally in all centrosaurines examined, and that in chasmosaurines (e.g., CMN 2245, 2280, ROM 843), this arching is much less pronounced. In addition, the deltopectoral crest of chasmosaurines is distinctly rectangular in outline, much more massive, and the insertion for the pectoralis muscle is located more distally. In centrosaurines, the pectoralis insertion is more proximal, and the smaller proximal head is distinctly narrower in outline proximally than it is distally.

Acknowledgments

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Table 1. Selected postcranial measurements (in mm) of *Styracosaurus albertensis.*

	Centrum length (max.)	Centrum width (max.)	Vertebra height (max.)
CMN 344			
Syncervical (1–3)	265	111	247
Cervical 4	67	115	254
Cervical 5	66	117	254
Cervical 6	64	114	274
Cervical 7	63	111	287
Cervical 8	63	106	300
Cervical 9	62	100	308
Thoracic 1	66	94	338
Thoracic 2	65	94	338
Thoracic 3	65	92	348
Thoracic 4	67	90	358
Thoracic 5	72	92	386
Thoracic 6	68	92	392
Thoracic 7	67	90	381
Thoracic 8	76	92	384
Thoracic 9	68	95	362
Thoracic 10	68	92	378
Thoracic 11	67	100	339
Thoracic 12	69	92	339
Caudal 1	65	80	252
Caudal 5	48	85	220
TMP 1989.097.001			
Cervical 5	–	97	161
Cervical 8	–	102	198
Cervical 9	–	97	193
Thoracic 5	–	98	326

	CMN 344		TMP 1989.097.001	
	Left	Right	Left	Right
Pectoral Girdle and Forelimb				
Scapula length	770	800	–	660
Scapula width (max.)	260	260	–	200
Coracoid length	–	360	–	210
Sternal plate length	–	340	–	–
Humerus length	595	630	510	500
Radius length	380	390	–	–
Metacarpal I	–	81	–	–
Metacarpal IV	105	–	–	–
Pelvic Girdle and Hind Limb				
Ilium length	–	1050	–	660
Ischium max. linear length	795	830	–	800
Prepubis length	–	–	–	350
Femur length	840	810	685	690
Tibia length	610	610	–	460
Fibula length	572	–	–	–
Metatarsal II	175	–	–	186

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